AVIAN BODY-SIZE CLUMPS AND THE RESPONSE OF BIRDS TO SCALE-DEPENDENT LANDSCAPE STRUCTURE IN SUBURBAN HABITATS

By

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Habitat selection is an important element in the spatial distribution and population dynamics of avian communities in heterogeneous landscapes. However, little empirical information exists about how birds respond to landscape structure at large scales. Previous research has shown that avian body-size clumps may reflect the hierarchical structure of landscapes. Body-size clumps are essentially groups of similar-sized adult birds that theoretically respond to structure at the same scale. The objective of this project was to test whether clumps reflect hierarchical landscape structure and whether they could be used to reveal at what scale different bird species are responding to suburban landscape structure.

Chapters 2 and 3 use a new statistical technique to determine whether avian body-size clumps exist for chosen faunal lists. In comparisons of avifauna lists derived from the same biome (temperate forest and boreal), results indicated that body-size clumps occurred at similar body-size ranges. This was interpreted as evidence that body-size clumps reflect the hierarchical structure of landscapes. In cross-continental comparisons, fewer European than eastern North American medium-sized bird species were present. European forests were historically much more fragmented than eastern North American forests. It was hypothesized that the fragmented European landscape contained disproportionately less resources for medium-sized birds.

In chapter 4, I explored at what scale birds in different body-size clumps responded to landscape structure during the summer and spring. From several North American suburban landscapes, I used the amount of tree canopy patches at four different spatial scales (0.2 km^2, 1.5 km^2, 25.0 km^2, and 85.0 km^2) to predict the variation of bird counts in these landscapes. Birds were grouped into body-size clumps determined for the temperate forest biome (Chapters 2 & 3). From multiple regression analyses, it was determined that birds of each size clump responded to tree canopy cover at different scales. The results provide a framework for researchers to conduct future research on how large-scale changes in the landscape affect different bird species. Also, the results can serve as guidelines to design suburban landscapes to attract a greater diversity of birds.

CHAPTER 1

INTRODUCTION AND OVERVIEW

Birds must respond to landscape structure at a variety of spatial scales (e.g., 1.0 m^2 to 1.0 km^2). The range of scales sampled by a bird is defined by the *spatial extent*, or largest area that is sampled by each bird, and the *spatial grain*, or minimum size of objects sampled by each bird (Kotliar and Wiens 1990, Wiens 1990). Throughout this dissertation, the term "response" is defined as the ability of a bird to "perceive" or utilize structure (e.g., tree canopy patches) in a landscape. Operationally, response is measured by the quantity of birds that occur in a particular area. The quantity of birds in a given area depends on whether sufficient structure (e.g., distribution of tree canopy patches, natural ground cover patches, or other vegetative features) exists at a scale range relevant to a particular species. Wiens (1989b) proposed that the range of scales pertinent to a particular bird species is dependent on the size of the bird. Theoretically, smaller birds respond to structure at smaller scales than larger birds. For example, to select a home range, a wren probably samples the distribution of individual bushes and trees whereas a hawk samples much larger groupings of trees (e.g., riparian habitat). However, exactly how large an area and what sizes of objects (e.g., trees and bushes) are sampled by different species is largely unknown. Few empirical studies address the range of scales relevant to different sizes of birds (Wiens 1995, Opdam 1991, Harrison 1992). In particular, empirical studies that address how birds or other organisms respond to structure at large scales (e.g., above the level of the home range) are virtually nonexistent (Lima and Zollner 1996).

The range of scales relevant to different organisms is difficult to measure. Hierarchy theory, though, could provide a framework to simplify such analyses. In hierarchy theory, complex ecosystems are decomposed into discrete hierarchical levels. Each level represents a scale at which biotic and abiotic factors interact much more strongly with each other than with other factors at other levels (Allen and Starr 1982, O'Neill et al. 1986). Hierarchical levels in an ecosystem can be defined by a *discontinuous* frequency distribution of process rates (Allen and Starr 1982, O'Neill et al. 1986, Holling 1992a) or by a *discontinuous* frequency distribution of object sizes in a landscape (O'Neill et al. 1986, Holling 1992b). Process rates (e.g., plant growth, fire regimes, erosion) are considered to be discontinuous when they operate at distinctly different temporal speeds (e.g., years, decades, centuries). Likewise, sizes of landscape objects (e.g., leaves, crown volume, stands of trees) are considered to be discontinuous when several modes appear in a frequency distribution of their sizes. Thus, each hierarchical level contains a specific category of processes and/or a defined size range of landscape objects.

A hierarchical organization of ecosystems has been inferred from empirical studies of landscapes and from models that captured the dynamic behavior of managed ecosystems (Allen and Starr 1982, O'Neill et al. 1986, Holling 1992a, Kent and Wong 1982, Bradbury and Reichelt 1983, Holling 1986). In some empirical studies of landscapes, fractal dimensions have been used to detect hierarchical levels (e.g., Kent and Wong 1982, Bradbury and Reichelt 1983). A fractal dimension measures the degree of complexity in a landscape, and significantly different fractal dimensions theoretically represent separate hierarchical levels. For example, Kent and Wong (1982) calculated two different fractal dimensions of lake shorelines. The fractal dimensions corresponded to glacial processes that shape lake shorelines at large scales and to erosional processes at smaller scales. In modelling studies, models were able to describe the dynamic behavior of several managed ecosystems with only 3-4 sets of variables (see review in Holling 1986). For example, boreal forest-insect dynamics could be described by the interaction of four dominant cycles (Holling 1992a). These cycles include a 3-5 yr cycle controlled by the interaction of insects, parasites, and needles; a 10-15 yr cycle caused by the interaction between insect defoliation and the regeneration of crown foliage that results in insect outbreaks within limited areas; a 35-40 yr cycle represented by the gradual growth of trees and insect outbreaks that cause tree mortality over an extensive area; and a > 80 yr cycle represented by a long successional period and tree longevity.

The above studies suggest that ecosystems could be hierarchically structured, but more independent tests are needed. If ecosystems were hierarchically organized, then separate groups of species may respond to structure primarily at different hierarchical levels (Holling 1992b). If so, Holling (1992b) hypothesized that animal masses would be grouped into several distinct "clumps." Clumps are essentially groups of similar-sized adult animals that are separated by significant gaps in a body-mass distribution. Body-size clumps are hypothesized to reflect both qualitative and quantitative structural properties of ecosystems. Different ecosystems would presumably have qualitatively dissimilar animal body-size clumps (i.e., the clumps would not match); differences in the clump structures theoretically reflect the unique landscape structure in a ecosystem. Also, the number of species in each clump could be dissimilar between different ecosystems; more species in a body-size clump is hypothesized to reflect a greater diversity of resources at a specific scale (Holling 1992b). A growing body of studies indicates that animal body-size clumps do reflect hierarchical structure in landscapes (see Holling et al. 1994). Thus, animal body-size clumps could be used as an "ecoassay" to measure both qualitative and quantitative landscape properties at a variety of scales.

Ecological systems to the human eye seem extraordinarily complex (Holling 1987), and it is a daunting task for ecologists to understand and measure ecological phenomena across multiple scales. As mentioned previously, it is especially difficult to determine the scales at which different species respond to landscape structure. For example, at what scale does the spatial distribution of trees determines whether a species is in a given area? One goal in this dissertation is to determine whether body-size clumps occur in avian body-size distributions. A second goal is to determine whether these clumps can be used to explore at what scales birds respond to structure in an environment. A third goal is to evaluate how body-size clumps can be used to measure the effect of suburban environments on avian species diversity and abundance. To accomplish these goals, I will take several steps:

Step (1) Chapter 2 uses a new statistical technique to detect clumps in avifauna lists from different regions in North America. The body-size clumps determined in this step hypothetically represent the underlying hierarchical structure of the temperate forest biome.

Step (2) In Chapter 3, avifauna lists from the boreal and temperate forest biome are compared between eastern North America and Europe. I hypothesize that within each biome, the body-size clumps should match if clumps reflect the hierarchical structure of landscapes. This step also provides further tests for the presence of body-size clumps of the temperate forest biome.

Step (3) In chapter 4, the size limits of the body-size clumps detected for the temperate forest biome (chapters 2 and 3) are used to place species into size categories. Each category theoretically represents a group of species that respond to landscape structure within the same range of scales. In suburban sites, variation in the percent of tree canopy cover (at four different scales) is used to predict the number of birds/hr censused for each body-size clump. Ultimately, for each clump, this analysis determines the scale(s) at which birds are responding to landscape structure.

Step (4) In chapter 5, a review is given of ecological studies conducted in suburban environments. Then, the results of chapter 4 are used to suggest how suburban landscapes could be designed to attract more species. Finally, I suggest how future empirical studies should be conducted to determine the scales at which birds respond to landscape structure.

Chapter 2 begins with a description of a new technique used to determine avian body-size clumps that theoretically represent the hierarchical structure of the North American temperate forest biome. The objectives of chapter 2 are 1) to determine whether avian body-size clumps exist for the North American temperate forest biome, 2) to determine whether body-size clumps match between a desert avian community and several temperate forest avian communities, and 3) to determine whether temperate forest avian communities and a desert avian community differ with respect to the number of species in each body-size clump. If body-size clumps reflect the hierarchical structure of landscapes, then body-size clumps should match between temperate forest avifauna lists whereas body-size clumps should not match between desert and temperate forest avifauna lists. The methodology and results from chapter 2 are basically the foundation for all other chapters. For example, the temperate forest body-size clumps discovered in chapter 2 were used to place censused suburban bird species (Chapter 4) into size categories (i.e., clumps) that theoretically represent groups of species responding to patches of canopy cover at the same range of scales.

However, the body-size clumps found in chapter 2 may, in part, be due to the degree of species overlap that inevitably occurred when I compared avian communities on the same continent (North America). Therefore in chapter 3, I compared the body-size clumps of New World and Old World avifauna from both temperate and boreal biomes. One objective of this chapter was to determine whether avifauna lists from similar biomes (but composed of entirely different species) had qualitatively similar body-size clumps. In other words, do the body-size clumps match between the avifauna lists from different continents? If body-size clumps reflect the hierarchical structure of landscapes, I predicted that body-size clumps should match between North American and European avifaunas (from the same biome).

While the avian body-size clumps should show an overall match, quantitative differences (i.e., the number of species in each clump) and qualitative differences (i.e., the position and number of clumps) probably exist between the North American and European avifaunas. Historically, changes in the pattern of North American and European landscapes have been quite different. Since the Pleistocene, European forests have been quite fragmented whereas North American forests have been quite extensive and continuous (Monkkonen and Welsh 1994). Because of this historical difference, I predicted that 1) fewer medium-sized birds would exist in Europe versus eastern North America, and 2) more clumps in the middle size range would appear in eastern North America than in Europe. I also compared the avian body-size clumps between the two biomes on the same continent. I predicted that body-size clumps within a small body-size range would display a better match than within a larger size range. The above predictions were based on the propositions that fragmentation would affect primarily medium-sized organisms (Morton 1990) and that different landscapes would be most similar at small scales (Holling 1992b).

In chapter 4, I explored at what scales birds (in different body-size clumps) responded to large-scale landscape structure when they choose home range areas during the summer and stopover/dispersing sites during the spring. Avian biologists have studied how birds respond to structure primarily at small scales (e.g., foraging decisions within a food patch); however, the spatial distribution of objects (such as tree patches) at large scales probably determines whether a bird occurs in a given area. Many ecologists have expressed the need for empirical studies of how species respond to structure at large scales (Lima and Zollner 1996, Wiens 1990, Wiens 1995, Opdam 1991, Harrison 1992). To simplify empirical analyses in chapter 4, I grouped birds into the temperate forest body-size clumps determined in Chapters 2 and 3. These body-size clumps are useful because birds in each body-size clump are theoretically responding to the same sizes of structural objects in a landscape within the same range of scales (Holling 1992b). I limited the scope of the study to only birds that forage or nest in the tree canopy. The objectives of chapter 4 are (1) to ascertain whether body-size clumps could be used to determine the scale(s) at which different sizes of birds make landscape-level decisions during the spring and summer, (2) to develop hypotheses about the spatial areas at which birds respond to large-scale landscape structure, and

(3) to develop hypotheses about the patch sizes within these areas that are sampled by birds of different sizes.

Chapter 5 is one of synthesis and speculation. The future survival of a vast range of animal species is intricately tied to the activities of humans because we are such a primary force of change in the environment. Suburban habitats are one way that humans have drastically altered the environment, and I emphasize the importance of conducting ecological research in these areas. I suggest that the size of a bird could be used to approximate the range of scales at which it responds to landscape structure. How different species of birds respond to habitat fragmentation is dependent on the range of scales relevant to each species (Wiens 1990, Kotliar and Wiens 1990). Many species may respond to structure within the same range of scales. Body-size clumps may represent categories of birds that respond to structure at similar scales. At large scales, once the spatial areas and patch sizes of birds are determined, then researchers may be able to predict which species will be most affected by human modifications of landscapes in suburban environments.

Further, body-size clumps could be used to determine the hierarchical structure of different ecosystems and amount of structure available to birds at different scales. This would be useful to urban wildlife managers. For example, if one knew that a majority of the species in an avian community occurred in one body-size clump, then a development could be designed to retain the scale-dependent landscape features pertinent to these sizes of birds. Overall, body-size clump analysis could guide researchers to the type of structure (at different scales) available to a particular size range of birds in a specific area. This would help researchers to design or restore features in suburban areas to increase the abundance and diversity of birds in these impacted landscapes.

CHAPTER 2

DETECTION OF HIERARCHICAL LANDSCAPE STRUCTURE USING DISCONTINUITIES IN AVIAN BODY-SIZE DISTRIBUTIONS

Introduction

A central question (and problem) in ecology today is the identification of the scales at which landscape patterns change in ecological systems (Levin 1992, Wiens 1989b, Pickett and White 1985, Dayton and Tegner 1984). Hierarchy theory may simplify studies that address this question because it decomposes complex ecosystems into discrete hierarchical levels (Allen and Starr 1982, O'Neill et al. 1986, Holling 1992a). A hierarchical level represents a scale at which biotic and abiotic factors interact much more strongly with each other than with other factors at other levels (Allen and Starr 1982, O'Neill et al. 1986). For example, a familiar ecological hierarchy is the organization of biological systems into different levels (e.g., cell, organism, population community, and ecosystem). Ecosystems can also be hierarchically organized. Hierarchical levels in an ecosystem are defined by *discontinuous* process rates (Allen and Starr 1982, O'Neill et al. 1986, Holling 1992a) or by a *discontinuous* frequency distribution of object sizes (e.g., tree patches) in a landscape (O'Neill et al. 1986, Holling 1992b). Process rates (e.g., plant growth, fire regimes, erosion) are considered to be discontinuous when they operate at distinctly different temporal speeds (e.g., years, decades, centuries). Likewise, from small to large spatial scales, sizes of landscape objects (e.g., leaves, crown volume, stands of trees) are considered to be discontinuous when several modes appear in a frequency distribution of their sizes. Thus, each hierarchical level contains a specific category of processes and may contain a defined size range of landscape objects.

A hierarchical organization of ecosystems has been inferred from empirical studies of ecosystems and from models that captured the dynamic behavior of managed ecosystems (Allen and Starr 1982, O'Neill et al. 1986, Holling 1992a, Kent and Wong 1982, Bradbury and Reichelt 1983, Holling 1986). In some empirical studies of landscapes, fractal dimensions have been used to detect hierarchical levels (e.g., Kent and Wong 1982, Bradbury and Reichelt 1983). A fractal dimension basically measures the degree of complexity in a landscape, and significantly different fractal dimensions theoretically represent separate hierarchical levels. For example, Kent and Wong (1982) calculated two different fractal dimensions of lake shorelines. The fractal dimensions corresponded to glacial processes that shape lake shorelines at large scales and to erosional processes at smaller scales. In modelling studies, models were used to describe the dynamic behavior of several managed ecosystems using only 3-4 sets of variables (see review in Holling 1986). However, these models and empirical studies may be a result of the way researchers make decisions or measure variables, not how ecosystems are actually structured. More independent tests are needed to establish whether ecosystems are hierarchically structured.

One independent test, proposed by Holling (1992b), states that if ecosystems were hierarchically organized, then gaps should appear in a distribution of animal body masses. Holling hypothesized that animal masses would be grouped into several distinct "clumps", reflecting the hierarchical structure of landscapes. Clumps are essentially groups of similar-sized adult animals that are separated by significant gaps in a body mass distribution. Animals in each body size clump are theoretically responding to the same sizes of structural objects in a landscape within the same range of scales because the size of an animal constrains the sizes of objects available to it (Holling 1992b). At this stage, the identity of the physical structure that a bird species is responding to is largely unknown. However, natural life history characteristics and the size of a species permits one to imagine what a species is probably responding to in a given landscape. Intuitively, different sizes of birds are responding to different types of structure in a landscape. For example, to select a home range, a wren probably samples the distribution of individual bushes and trees whereas a hawk samples much larger groupings of trees (e.g., riparian habitat).

Body-size clumps are hypothesized to reflect both qualitative and quantitative structural properties of landscapes. Different landscapes would have qualitatively dissimilar animal body-size clumps (i.e., the mass ranges of clumps from different landscapes would not match); differences in the clump structures theoretically reflect the unique hierarchical organization in each ecosystem. Also, the number of species may be dissimilar in clumps of different ecosystems; more species in a body-size clump are hypothesized to reflect a greater diversity of resources at a specific scale (Holling 1992b). Holling (1992b) formally stated this theory as:

> "*The Textural-Discontinuity Hypothesis:* Animals should demonstrate the existence of a hierarchical structure and of the discontinuous texture of the landscape they inhabit by having a discontinuous distribution of their sizes, searching scales, and behavioral choices. Landscapes with different hierarchical structures should have corresponding differences in the clumps identified by such a bioassay."

Testing this hypothesis, Holling (1992b) found that bird faunas of the boreal forest, of the short-grass prairie, and pelagic birds of the pacific northwest were grouped into several statistically distinct body-size clumps. Birds in these different ecosystems had dissimilar clump structures; the differences in the clump structures seemed to reflect qualitative and quantitative landscape differences in each ecosystem. For example, the smallest clump category was absent in the short-grass prairie, but it was present in the boreal forest (qualitative difference). Also, fewer species were present in the smaller-sized clumps of the short-grass prairie than in the smaller-sized clumps of the boreal forest (quantitative difference). These differences probably reflect the greater diversity of fine textures distributed through the boreal forest tree canopy, whereas the prairie has a much smaller amount of fine textures distributed just above the ground.

Although the above results are consistent with the textural-discontinuity hypothesis, other alternative hypotheses exist to explain the observed avian body-size clumps (see Holling 1992b for review). Other hypotheses include 1) "*The "Urtier Historical Hypothesis*": current animal sizes could be historically constrained by a limited number of ancestral forms, and these ancestral forms were already in discrete size ranges independent of landscape structure; 2) "*The Limited-Morph Hypothesis*": the number of life-forms (such as the hovering ability of a hummingbird vs. the soaring ability of a vulture) are limited, and this limitation constrained the size ranges of animals; and 3) "*The Trophic-Trough Hypothesis*": trophic interactions (e.g., predator/prey interactions) may maintain discontinuities in body masses because there is a relationship between the size of an organism and what it eats. Holling (1992b) tested these hypotheses by comparing body-mass clumps in different ecosystems and by comparing different animal taxa (birds vs. mammals) or animals with different feeding strategies (carnivores vs. herbivores). From these analyses, only the textural-discontinuity hypothesis resisted disproof. Thus, animal body-size clumps could be used as an "ecoassay" to measure both qualitative and quantitative landscape attributes relevant to birds at a variety of scales. This possibility is explored for North American temperate forest avifauna in this chapter.

Holling's original tests for animal body-size clumps did demonstrate that different animal communities displayed discontinuities in body-size distributions, but these analyses were based on visualization techniques that were somewhat subjective (e.g., eye-balling how clumps matched between animal lists) and have been criticized in the literature (Manly 1996). Although visualization can be as valid as statistical inference (Cleveland 1993), formal statistical tests are more accepted in the scientific community. Also, discontinuities in body-size distributions could be caused by chance alone, and this issue was not adequately addressed in Holling's original paper. A goal of chapter 2 was to utilize and describe a new statistical technique and methodology to determine clumps in animal body-size distributions. A second goal was to use additional faunal lists to further test the textural-discontinuity hypothesis. The objectives of this goal were 1) to determine whether avian body-size clumps exist for the North American temperate forest biome, (2) to ascertain whether a desert avian community and several temperate forest avian communities have similar body-size clumps, and 3) to determine whether temperate forest avian communities and a desert avian community differ with respect to the number of species in each body-size clump.

If body-size clumps reflect (*qualitatively*) the hierarchical structure of landscapes, then body-size clumps should match between temperate forest avifauna lists. However, between desert and temperate forest avifauna lists, body-size clumps should not match at all. In all of the above comparisons, I hypothesized that most of the mismatch between body-size clumps would be present at the medium to large size range. Small-scale structure is probably geometrically the same regardless of the landscape concerned (Holling 1992b). For example, bushes, trees, or small patches of herbaceous ground cover may have the same geometric attributes from one landscape to the next. Thus, I predicted that the number and location of body-size clumps at the smaller size range will be similar even when the temperate forest and desert avifauna are compared.

Further, if body-size clumps reflect (*quantitatively*) the diversity of resources at different hierarchical levels, then the desert avifauna (compared to the temperate forest avifauna) should contain relatively fewer species in the smaller size range. This prediction is based on previous results that structurally simpler landscapes had fewer small species (Holling 1992b). The rationale is that the vertical height diversity is severely limited in deserts relative to temperate forest regions. This would decrease the diversity of resources available to small birds, resulting in fewer desert species.

The above predictions are contingent on several underlying assumptions. First, in a avifauna list, birds are considered to primarily utilize structure within the boundaries of a chosen landscape (e.g., a temperate versus a desert biome). Second, the "boundaries" of a landscape are assumed to be accurately and consistently defined in the literature. Third, when one compares avifauna lists derived from different areas that are assumed to be similar (e.g., different regions within the temperate forest biome), it is assumed that the selected areas are "truly" similar in terms of the physical landscape structure. Fourth, reported masses of individual bird species is assumed to represent the true size of a species. If any of these assumptions are violated, then the outcome of an analysis could be incorrect. Thus, care should be taken in selecting a landscape and assembling a avifauna list.

Methods

In this section, I first describe a methodology and statistical technique for identifying significant clumps in animal body-size distributions. Second, I applied this methodology to several avifauna lists of the temperate forest biome and of the desert biome. This second step tests whether the body-size clumps theoretically represent a hierarchical structure that is characteristic of the temperate forest biome. Third, I compared the number of species (within certain size ranges) among different ecoregions. This third step addresses whether the diversity of resources are different between different ecoregions of North America.

Methodology of Clump Analysis

If body-size clumps reflect the underlying hierarchical structure of landscapes, then I predicted that

(1) the distribution of body sizes in faunal lists should contain body-size clumps rather than be continuous,
(2) faunal lists from similar landscapes should have body-size clumps in the same size ranges, and
(3) faunal lists from different landscapes should have body-size clumps in different size ranges.

But how does one first objectively determine whether clumps exist in a body-size distribution (prediction 1)? Then, how does one test predictions 2 and 3? Current statistical techniques cannot address prediction 1 effectively because available clustering methods cannot reliably identify the correct number of clusters (i.e., clumps) in data sets (see reviews in Milligan and Cooper 1985, Bock 1985). Further, no techniques have been developed to address predictions 2 and 3. A new technique had to be developed. The steps outlined below are a result of a four year process of trial and error with examining various data sets, using different statistical techniques, and computer simulation. Much of the work was conducted by Paul Marples who tenaciously worked on this problem and developed the procedure outlined below.

This procedure uses inferential statistics, but it is not conventional. It does answer the question whether chosen faunal lists contain body-size clumps, and whether faunal lists have similar or different body-size clumps. However, it is much more problematic to estimate the "true" number of clumps that theoretically reflect the underlying hierarchical structure of a particular landscape. In this case, the method is meant more as a heuristic approach to guide researchers to what the "true" number of clumps is in a body mass distribution. To gain more confidence in a determination of the number of clumps for a particular landscape type (e.g., deserts), multiple data sets need to be analyzed. If multiple data sets reveal a consistent number of clumps, then one can be more confident what number of clumps theoretically reflect the hierarchical organization of a particular landscape type.

Step 1. The purpose of this step is derive faunal lists that can be used to address predictions 1, 2 and 3 (above). If one wants to test whether faunal lists from similar landscapes have similar body-size clumps, then faunal lists should be derived from regions that theoretically would have the same landscape structure. Conversely, if one wants to test whether faunal lists from different landscapes have different body-size clumps, then faunal lists should be derived from regions that theoretically would have different landscape structure.

But what scale should represent a landscape and its accompanying faunal list? Landscapes at the biome level (e.g., desert vs. forest) are the most drastically different (at least to our eye); thus it is reasonable to compare faunal lists that represent a particular biome. However, for any comparison, the fewer number of species shared between the faunal lists, the better. A large degree of species overlap may bias the analyses to find the same clumps because they share too many species. This is no problem when comparing faunal lists from different biomes (i.e., testing prediction 3), but it is a problem when comparing faunal lists that represent the same biome (i.e., testing prediction 2). One way to minimize species overlap is to compare faunal lists from different continents (but the same biome). Another way is to compare faunal lists derived from different ecoregions within a biome. The basic difference between biomes and ecoregions is a matter of scale. At the largest scale (i.e., biome level), classification is largely based on climatic factors (e.g., annual rainfall). At smaller scales (e.g., ecoregion), the classification is based on vegetational macrofeatures along with climatic factors (Baily 1995, Omernik 1987). Ecoregions within the same biome theoretically share similar hierarchical properties specific to that biome. I therefore hypothesize that avian body-mass clumps will be similar among ecoregions within a biome. A comparison between ecoregions from the same biome could be used to test prediction 2.

Step 2. The purpose of this step is to establish whether chosen faunal lists are "clumpier" than expected by chance alone. This test, called the Gap Rarity Index (GRI) does not estimate the true number of lumps because it relies on avoidance of Type I errors (i.e., alpha = 0.05). The true number of clumps may actually be more if power was taken into account. The number of clumps determined in this step are regarded as a *minimum* number of clumps that are likely for a given faunal list.

First, a faunal list is arranged from the smallest species to the largest species, and the log mass is calculated for each of the species. All bird masses (in grams) are derived from Dunning's (1992) book of avian body masses; the mass for each species is the mean mass of reported male and female averages. Between each consecutive species, the size of the "gap" is calculated by taking the mass of species $_{(i+1)}$ - species $_{(i)}$. One obtains a variety of observed gap sizes where larger gaps may indicate divisions between clumps. But which gap sizes are larger than what would occur by chance alone?

To answer this, simulated data sets are randomly sampled from a unimodal distribution (the sample size is kept constant between the observed and the simulated data sets). A unimodal distribution (i.e., lognormal distribution) is calculated by taking a kernel estimate for an observed data set. A kernel estimate is simply a smoothed histogram (Silverman 1986). A single parameter (h), similar to the bin-width of a histogram, controls the amount of smoothing in a data set. This parameter is decreased just enough to give one mode (i.e., unimodal) and no more (Silverman 1986, Manly 1996). This unimodal distribution represents a null model where no discontinuities exist in a body-size distribution.

From this unimodal distribution, 10,000 simulated data sets are generated. A distribution of expected gap sizes are calculated from the simulated data sets. Thus for each observed gap, 10,000 simulated gaps are generated. These simulated gaps represent a range of gap sizes that could occur by chance alone. An observed gap is considered to be significant when a large number of the simulated gap sizes is less than the observed gap size. Conventionally, a significant number is where 9,499 of the simulated gap sizes are less than the observed gap size (i.e., alpha = 0.05). For each observed gap, one can determine its significance by comparing it to the simulated gap sizes.

Step 3. The purpose of this step is to determine whether chosen faunal lists have similar body-size clumps (i.e., do the size intervals match?). This step is used to further test the textural-discontinuity hypothesis and to guide researchers to the number of clumps that theoretically reflect the underlying hierarchical landscape structure. If body-size clumps reflect the hierarchical organization of different landscapes, then similar landscapes should have similar body-size clumps and different landscapes should have different body-size clumps. One compares a variety of combinations of numbers of clumps in each data set above or equal to the minimum number of clumps determined in step 2. The question addressed is whether a significant match occurs when a variety of combinations are compared (e.g., 7 vs. 8, 8 vs. 10, etc.). Each comparison represents a proposed model that could result in a significant "match" (if at all). A significant match (or matches) indicates that the data sets are similar in terms of where the clumps appear in a body-mass distribution. Below, the procedure to test whether chosen faunal lists match is outlined.

For simplification, this procedure will be discussed in terms of a pair-wise comparison, but a three-way or *n*-way comparison can be done. As mentioned in step 2, each faunal list is arranged from the smallest species to the largest species, and the log mass is calculated for each of the species. A kernel estimate (Silverman 1986) is then used to calculate a variety of frequency distributions for each faunal list (e.g., 2 modes, 3 modes, 4 modes, etc.). A specified number of modes are made by varying the smoothing parameter (h) to one particular value; the parameter is decreased just enough to give the specified number of modes and no more (Silverman 1986, Manly 1996). We found that frequency distributions of 2 to 15 modes (i.e., clumps) are a sufficient range to explore for most data sets.

Once the frequency distributions have been calculated, these distributions are then defined in terms of clumps and gaps. Clumps are the interval around each mode in a distribution defined by the inflection points that give maximal and minimal slope (Figure 2-1). All other intervals in a distribution are defined as gaps.

Across the chosen faunal lists, all combinations of clumps (equal to or above the lower limit determined in step 2) are compared to determine the degree of mismatch (**m**) for each comparison. The number of clumps determined in step 2 are

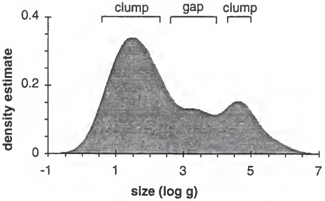


Figure 2-1. A hypothetical data set fitted with a 2 mode kernel estimate (the units for the density estimate is the percent area under the curve within a defined mass range). Each clump is defined by inflection points that give maximal and minimal slope. Maximal and minimal slopes are mathematically calculated.

considered to be a conservative estimate (i.e., controlling for Type 1 error), and more modes may actually exist in a distribution. For each comparison, the degree of mismatch (m) is calculated by adding the proportion of gaps filled by lumps (P_{gl}) and the proportion of lumps filled by gaps (P_{lg}):

$$\mathbf{m} = P_{gl} + P_{lg}$$

Because **m** is a summation of two proportions, m can vary between 0 and 2 where 0 is a perfect match and 2 is complete mismatch. This technique is similar to a phi correlation index (see Wherry 1984). Unlike the phi correlation index, though, the degree of mismatch (m) is better at detecting significant matches between data sets. For each model, the observed mismatch is set aside to be compared to mismatches calculated from models of simulated data sets drawn from a unimodal distribution.

To distinguish between significant matches and spurious ones, a distribution of expected mismatches (drawn from a unimodal distribution) for each proposed model is computed (see paragraph below). In other words, what is the probability that each observed mismatch could have occurred by chance alone? Expected mismatches represent the degree of mismatch expected when several data sets (each drawn from a unimodal distribution) are compared to each other for a given model. A significant match occurs in the real data set when a large number of the expected mismatches is more than the observed mismatch of a particular model. The outline below describes how to generate the expected mismatch values for each proposed model.

First, a unimodal distribution is calculated with a kernel estimate that gives one mode for each observed data set. This unimodal represents a null model where no discontinuities exist in a body-size distribution. From this unimodal distribution, simulated data sets are randomly sampled (the sample size is kept constant between the observed and the simulated data sets). For these simulated data sets, expected mismatch values are calculated for each model (e.g., 7 vs. 7 clumps, 8 vs. 9 clumps, etc.) as explained above. At least 10,000 potential mismatches are calculated for each model by randomly comparing the simulated data sets 10,000 different times. For a given model's distribution of expected mismatches, a critical value can be determined. For example, at 0.05 (i.e., alpha = 0.05), a critical value is where 9,499 expected mismatch values are greater than this value. Thus, for each proposed model, we can determine the significance of its observed mismatch value by comparing it to the critical mismatch value. A null hypothesis states that the observed mismatch value of a model is no different from the critical mismatch value generated from a unimodal distribution. A model that gives an observed mismatch value at or below the critical mismatch value (alpha = 0.05) is considered to be significant.

Step 3 can be used as a heuristic tool to determine what the "true" number of clumps is for a given landscape (i.e., reflecting the underlying hierarchical landscape structure). It should be emphasized that the only way to determine the "true" number of clumps for a given landscape type is to look at the matching between faunal lists that theoretically represent the same underlying hierarchical organization. If only one match resulted from comparing faunal lists derived from the same landscape, this match may represent the underlying hierarchical landscape structure. However, for some comparisons, more than one model may give a significant match. When several different models match, one can tentatively select the one model that has the most equitable number of clumps (between the data sets). The rationale is that faunal lists from the same landscape type should have a similar number of clumps because each list is a theoretical representation of the same hierarchical landscape structure. Even if a model is selected, this selection is tentative and more independent evidence is needed. Additional faunal lists (representing the same landscape type) should be compared to determine whether a similar match exists.

One additional point should be mentioned when comparing faunal lists derived from the same landscape type. Recall that the idea in these comparisons is to ascertain whether body-size clumps reflect the hierarchical organization of a landscape. Chosen faunal lists usually represent landscapes at the biome or ecoregion level. At such large scales, some landscape variation exists between virtually any comparison. This holds true for faunal lists derived from the same biome on different continents and for faunal lists taken from ecoregions within the same biome. Even though this variation exists, landscapes from the same biome probably contain similar hierarchical organization at the biome level. A significant overall body-size clump match would theoretically be a reflection of this biome-level organization. However, within some size ranges, the body-size clumps may not line-up as well as in other places. Where clumps do not line-up as well may be an indication of the unique landscape structure of a particular ecoregion or biome. Thus, comparing faunal lists representing the same landscape type will not only reveal (theoretically) hierarchical similarities but also differences. Where differences occur theoretically reflect the scales at which structural differences exist between landscapes.

The above interpretations presume that none of the underlying assumptions have been violated. As stated earlier, these assumptions are 1) birds of each list are considered to primarily utilize structure within the boundaries of a chosen landscape, 2) the "boundaries" of a landscape (e.g., temperate forest biome) are accurately and consistently defined in the literature, 3) areas that are selected to be similar are "truly" similar in terms of the physical landscape structure, and 4) reported masses of individual bird species is assumed to represent the true size of a species. If any of these assumptions are violated, then the interpretation of an analysis could be incorrect.

Step 4. The purpose of this step is to group species into their appropriate clumps. If a significant match is determined and one particular model was selected (step 3), then the size range of each body-size clump is defined by the inflection points that give maximal and minimal slopes (i.e., edges: see step 3). However, some species occur outside these intervals (i.e., in the gaps). One usually wants to compare the quantity of species in each clump using the full species list. It is useful to group species in each gap interval into either the upper or lower clump. To do this, the midpoint of the largest gap in the body masses between two species (in this gap interval) is used as the dividing line; species to the left of this midpoint are placed in the lower clump and species to the right of this midpoint are placed in the upper clump. Thus, the upper and lower masses of a reported body-size clump are not the "statistical" edges (those are the inflection points), but they theoretically represent a size range of species that respond to structure within the same range of scales.

In addition, even when the body-size clumps of faunal lists match statistically, the upper and lower masses of these clumps usually do not line-up exactly; thus, it is somewhat problematic to construct body-size clumps that represent all of the analyzed data sets. The reason why clumps do not line-up exactly between faunal lists (assuming that each faunal list represents the same underlying hierarchical landscape structure) is that each faunal list represents an *approximation* of underlying landscape structure at the biome level. As explained earlier, even landscapes from within the same biome would contain some structural differences. Given this, one should not expect an exact match between different faunal lists.

To construct a representative body-size clump pattern for all faunal lists, the following is done. First, the body-size clumps of each faunal list are arranged from the smallest to the largest clump (i.e., clump 1, clump 2, etc.). Then, the same clump (e.g., clump 1) is compared across the data sets. If two or more data sets had clumps that lined-up exactly, then this mass range marks the upper and lower masses of this clump. When none of the upper and lower masses of a specific clump lined-up, then an average of the upper and lower masses (across all faunal lists) is used to delineate the "size range" of this clump.

Clump Analyses of North American Temperate Forest Avian Communities

An hypothesis tested here was whether a match occurred between body-size clumps from different ecoregions of the temperate forest biome. A significant match would be consistent with the hypothesis that body-size clumps reflect the hierarchical organization of a particular biome (in this case, the temperate forest biome). Also, even if an overall significant match resulted between the different ecoregions, it was hypothesized that most of the mismatch would be present at the medium to large size range. As mentioned previously, small-scale structure is probably geometrically the same regardless of the landscape concerned; body-size clumps at the smaller size range will be similar when avifauna from different ecoregions are compared. I followed the outline (see above methodology of clump analysis) to determine whether matching occurred between body-size clumps of different avifauna lists of the North American temperate forest biome.

I could have selected any ecoregion in the North American temperate forest biome, but I selected areas where researchers had conducted suburban bird surveys in several cities. The main reason I selected areas based on the location of suburban surveys is that in Chapter 4, I use these suburban surveys to estimate the scales at which birds in different body-size clumps respond to landscape structure. However, I first had to determine whether avian communities in these different suburban areas could be grouped into similar body-size clumps. These body-size clumps were determined in this chapter.

I constructed bird faunal lists based on the geographic location of each city (hereafter called regional bird lists). These regional bird lists were all landbird species, excluding exotics, that could hypothetically breed within each suburban area (i.e., their breeding ranges overlapped with the exact locations of surveys conducted in a suburban area). These regional bird lists were used to establish a body-size clump pattern that hypothetically reflects structure of a landscape before a human-caused transformation occurred. It should be noted that all birds that historically could breed in a given area were included in the avifauna lists, even if the birds had been locally extirpated due to human activity. All bird masses (in grams) were derived from Dunning's (1992) book of avian body masses; for each species, the mass used was the mean mass of both reported male and female averages. Sites selected were Amherst & Springfield, MA (DeGraaf and Wentworth 1981); Austin, TX (Sexton 1987); Blacksburg, VA (Lucid 1974); Chicago, IL (Guth 1980); Seattle, WA (Penland 1984); and Vancouver, B.C. (Lancaster 1976; Weber 1972). Based on Odum's (1971) map of the major biomes of the world, all of the cities are located in the temperate forest biome. The cities are located in five different ecoregions of this biome: Amherst & Springfield - Northeastern Highlands; Austin - Texas Blackland Prairies and Central Texas Plateau; Blacksburg - Central Appalachian Ridges and Valleys; Chicago - Central Corn Belt Plains; and Seattle & Vancouver - Puget Lowland (Omernik 1987). A qualitative vegetative and climatic description of each ecoregion is given in Table 2-1.

Only the regional avifauna lists that had minimal species overlap were used to determine whether body-size clumps matched for regions in the temperate forest biome. Several of the regional avifauna lists shared a considerable amount of bird species (70% or higher overlap). However, the Amherst, Austin, and Vancouver regional lists had a species overlap of 50% or less. Only these three data sets were used in the subsequent clump analysis. Steps 2 - 4 were followed as described above (see clump analysis).

Table 2-1. A qualitative vegetative and climatic description of six different ecoregions of North America. Source: Bailey, 1995 and Omernik 1987.

City	Ecoregion	Avg. annual rainfall	Vegetation
Amherst, Springfield	Northeastern Highlands	35 - 60 inches	Deciduous forest dominated by tall broadleaf trees; high flora diversity; high vertical height diversity
Austin	Texas Blackland Prairies and Central Texas Plateau	10 - 30 inches	Semi-arid and subtropical savanna woodland; pinyon-juniper woodland; scrub oak; mesquite; medium - low flora diversity; medium - low vertical height diversity
Blacksburg	Central Appalachian Ridges and Valleys	35 - 60 inches	Deciduous forest dominated by tall broadleaf trees; high flora diversity; high vertical height diversity
Chicago	Central Corn Belt Plains	30 - 40 inches	Deciduous forest dominated by oak-hickory in dry areas and beech-sugar maple in wet areas; medium-high flora diversity; medium-high vertical height diversity
Seattle, Vancouver	Puget Lowland	30 - 50 inches	Coniferous lowland mixed with deciduous trees (big-leaf maple, oregon ash, douglas fir); medium-high flora diversity; medium-high vertical height diversity
Tucson	Southern Basin and Range	2 - 10 inches	Arid landscape, sparse vegetation consisting of cacti, shrubs, creosote bush, open stands of trees; low flora diversity; low vertical height diversity

Comparison Between the Clumps of a Desert and Several Temperate Forest Avian Communities

The hypothesis tested here was whether avian body-size clumps from different biomes would match. It was predicted that a clump analysis between desert and temperate forest avifauna would reveal no significant match. No match would be evidence in support of the hypothesis that body-size clumps do reflect the hierarchical "landscape signature" of biomes. However, even though an overall mismatch may occur, it was predicted that body-size clumps at the smaller size range will match between a desert and a forest avian community. As mentioned previously, this is because small scale structure is probably geometrically similar even between different landscapes.

A regional avifauna list from Tucson, AZ was compared to the Amherst, Austin, and Vancouver regional avifauna lists. I selected Tucson because a suburban survey was also conducted in this city (Mills et al. 1989). For the purposes of this study, I could have selected several different areas in the Southwest region of the U.S., but I selected an area where a suburban study was conducted. This was done to gather data the same way it was gathered for the temperate lists. Essentially the Tucson avifauna list represents an ecoregion of the desert biome and the Amherst, Austin, and Vancouver avifauna lists represent ecoregions of the temperate forest biome. Again, Steps 2 - 4 were followed as described above (see methodology of clump analysis).

Densities of Species in Body-size Clumps of Each Ecoregion

The above five ecoregions of the temperate forest biome and the one ecoregion of the desert biome may contain different amounts of resources at different scales. The body-size clumps determined from the above analysis are hypothesized to represent groups of birds that respond to the same sizes of landscape attributes within the same range of scales. Therefore, the number of species occurring in each body-size clump of a region is theoretically reflecting the diversity of resources available to birds at certain scales. I compared how similar the number of species in each body-size clump was among the ecoregions of the temperate forest biome. I also compared the Tucson avifauna to the other temperate forest avifauna. I first determined how many Tucson species fit into each body-size clump determined for the temperate forest biome. I did this because I had to use similar size ranges in order to compare the number of species in the Tucson region versus the other ecoregions. G-tests were used to detect significant differences (alpha = 0.05).

Based on the vegetative and climatic characteristics (Table 2-1), I hypothesized that the Tucson and Austin avifauna list would have relatively fewer number of small birds than the other ecoregions. I made these predictions based on previous results that structurally simpler landscapes had fewer small species (Holling 1992b), and on earlier work that found bird diversity increased with an increase in foliage height diversity (MacArthur 1972, Recher 1969). The rationale is that the vertical height diversity is severely limited in Tucson and somewhat limited in the Austin area (relative to the other ecoregions). This would decrease the diversity of fine-texture resources available to small birds, resulting in a fewer number of small birds in the Tucson and Austin area.

Results

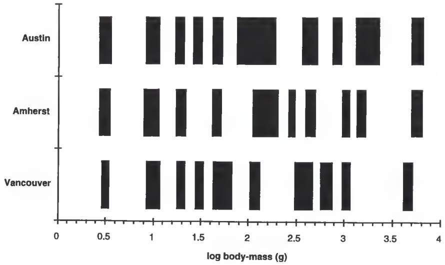
Body-size Clumps of the Temperate Forest Biome

From the Gap Rarity Index (GRI), all of the ecoregions displayed a significant number of clumps (Table 2-2). Looking at all combinations of 8 clumps and above (the minimum detected for each ecoregion), the Amherst, Austin, and Vancouver comparisons resulted in several significant models: a 14-9-8, 14-10-8, 14-10-9, and 10-10-10 (clumps in Amherst, Austin, and Vancouver, respectively) displayed significant matches ($P < 0.05$). The 10-10-10 model was chosen to represent the underlying hierarchical landscape structure (because it was the most equitable). The clump and gap intervals are displayed in Figure 2-2. Comparing the position of the clumps (by eye) for the 10-10-10 model, most of the mismatch occurred in the medium to large size range from $10^{1.3}$ to $10^{3.5}$ grams (Figure 2-2). At $10^{1.5}$ grams, the Amherst faunal list did not have a clump whereas the Austin and Vancouver lists did at this mass. Also, the Amherst faunal list had a clump at around $10^{2.5}$ grams whereas the Austin and Vancouver lists did not have a clump at this mass. Between $10^{2.5}$ grams and $10^{3.5}$ grams, a minor amount of

Table 2-2. Number of body-size clumps detected for each ecoregion from the Gap Rarity Index.

Ecoregion	Number of Clumps
Amherst	9 *
Vancouver	8 *
Austin	9 *
Tucson	8 *

* $P < 0.05$



Clump and gap intervals of bird body-mass data (10 lump model)

Figure 2-2. Body-size clump structure of three different ecoregions of the North American temperate forest biome (Austin, TX; Amherst, MA; Vancouver, B. C.).

mismatch also occurred; Austin had a large clump around $10^{3.2}$ grams, Amherst had a smaller clump, and Vancouver did not have a clump. Body-size clumps at $10^{1.3}$ grams and below seemed to match among the three faunal lists.

For the 10-10-10 model, the size range of each clump (defined by the upper and lower masses) are listed in Table 2-3. For ease of reporting the results, the 10 size categories were assigned numbers in ascending order starting with 1 for the smallest size category (0.0 - 6.9 grams) to 10 for the largest size category (greater than 2080.5 grams). This 10-10-10 model may reflect the underlying hierarchical landscape structure of the temperate forest biome. Chicago, Seattle, and Blacksburg are located in the temperate forest biome and they had quite a large degree of species overlap with the Vancouver and Amherst avifauna list. Thus, their avifauna regional lists are also proposed to have 10 body-size clumps.

Amherst, Vancouver, Austin (Temperate Forest Biome) vs. Tucson (Desert Biome)

Looking at all comparisons of 8 clumps and above, no significant match was found for the Austin vs. Tucson and Vancouver vs. Tucson comparisons ($P > 0.05$). However, several significant matches were found for the Amherst vs. Tucson comparison: 8-8, 9-9, and 10-10 ($P < 0.05$). For the 10-10 model, the clumps and gaps are displayed in Figure 2-3. Among the four avifauna lists, body-size clumps at $10^{1.3}$ grams and below seemed to match quite well, but a larger degree of mismatch occurred at clumps above $10^{1.3}$ grams

Table 2-3. Size ranges for each of the 10 avian body-size clumps determined from the Amherst, Vancouver, and Austin comparison.

Bird-size Category	Size Range (g)
1	0-6.9
2	7.0-16.5
3	16.6-21.6
4	21.61-33.75
5	33.76-61.6
6	61.7-115.0
7	115.1-184.0
8	185.0 - 576.5
9	577.0-2080.5
10	> 2080.5

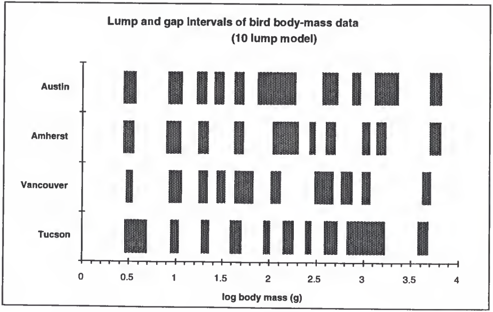


Figure 2-3. Avian body-size clump structure of four different ecoregions; Tucson avifauna regional list is in the desert biome and the Amherst, Vancouver, and Austin avifauna regional list are in the temperate forest biome.

(especially for the Tucson vs. Vancouver and the Tucson vs. Austin comparisons).

Species Densities in Each Body-size Clump

Using the 10 clump model, the number of species in each body-size clump was quite similar for the ecoregions of the temperate forest biome. However, the Austin ecoregion, as predicted, had the fewest number of category 2 species than the other temperate forest sites (Table 2-4), but this was not statistically significant ($P > 0.05$). In the Tucson ecoregion (desert biome), the number of species in bird-size category 2 was significantly less than in the other temperate forest ecoregions ($P < 0.05$), except for the Tucson vs. Austin comparison ($P > 0.05$). In addition, the Tucson ecoregion had more species in bird-size category 5 when compared to the temperate forest ecoregions (Table 2-3), but this was only statistically significant for the Seattle/Vancouver vs. Tucson comparison ($P < 0.05$).

Table 2-4. Number of species recorded for each bird-size category from North American avifauna lists.

Bird-size Category	Size Range (g)	Seat	Vanc	Amh	Blac	Chic	Aus	Tuc
1	0.0 - 6.9	5	5	3	2	2	3	6
2	7.0 - 16.5	26	25	29	21	25	17	13
3	16.6 - 21.6	9	9	16	12	17	12	7
4	21.61 - 33.75	10	8	14	11	13	13	11
5	33.76 - 61.6	9	9	13	12	13	11	20
6	61.7 - 115.0	11	10	11	11	14	11	9
7	115.1 - 184.0	7	7	6	5	7	8	9
8	185.0 - 576.5	9	8	6	9	12	4	6
9	577.0 - 2080.5	10	10	5	4	4	5	10
10	> 2080.5	1	1	1	2	1	2	1

Seat = Seattle, WA; Vanc = Vancouver, B.C.; Amh = Amherst, MA; Blac = Blacksburg, VA; Chic = Chicago, IL; Aus = Austin, TX; and Tuc = Tucson, AZ.

Discussion

Bird body-size distributions were shown to be discontinuous (i.e., "clumpy") by the Gap Rarity Index. Further, the Amherst, Vancouver, and Austin avifauna lists (temperate forest biome) had body-size clumps at similar body-size ranges. If the clumps had not matched, then there would be little support for the textural-discontinuity hypothesis (i.e., similar landscapes having similar body-size clump patterns). Further, the body-size clumps between Tucson (desert biome) and Amherst, Austin, and Vancouver (temperate forest biome) demonstrated that two of the three comparisons did not match. The Vancouver/Austin vs. Tucson comparison did not show a significant match, but the Amherst vs. Tucson comparison did. The mismatch between at least two of the comparisons between different biomes is consistent with the textural-discontinuity hypothesis (i.e., different landscapes having different body-size clumps). However, the one significant match between the avifauna of different biomes suggests that 1) body-size clumps may not reflect the hierarchical structure of landscapes, 2) the hierarchical structure of biomes may be quite similar at a variety of scales, or 3) errors occurred in the construction of the avifauna lists (e.g., reported masses were incorrect or the avifauna lists did not accurately contain only those species that breed in each respective area). In addition, other alternative hypotheses (as mentioned in the intro.) may explain body-size clumps (see Holling 1992b for review). To further address the textural-discontinuity hypothesis, future studies should continue comparing faunal lists from different biomes to see whether significant or non-significant matches occur.

Body-size Clump Matches

The 10 clump model found in the Amherst, Austin, Vancouver comparison may represent the hierarchical landscape "signature" characteristic of the temperate forest biome. However, it is still tentative whether body-size clumps reflect hierarchical landscape structure. Nevertheless, if body-size clumps do reflect landscape structure, then where clumps do not match may be an indication of the scales at which structural differences exist. The 10 clump model was used to see how well the body-size clumps matched between the different ecoregions.

The Amherst, Vancouver, and Austin comparison did reveal, as predicted, that the body-size clumps at the smaller size range ($10^{1.3}$ grams and below) were the most similar. Even the Amherst/ Vancouver/Austin versus Tucson comparison showed that the body-size clumps at the smaller size range matched. These results suggest that to some degree, small-scale structure from landscape to landscape may be geometrically similar. That is, the frequency distribution of landscape objects at small scales could be the same regardless of the landscape type. For example, perhaps the physiognomy and the spatial distribution of small bushes, trees, and herbaceous ground is similar. This is only one example, though; many more avifauna body-size distributions need to be compared to see whether body-size clumps at the smaller size range are consistently the most similar.

Although there was an overall significant match between the Amherst, Vancouver, and Austin avifauna lists, the medium to large size range ($10^{1.3}$ to $10^{3.5}$ grams) displayed some degree of mismatch. One explanation may simply be that this mismatch is a result of sampling error. The measurements of body mass or the construction of the avifauna lists may have introduced enough variability to cause the body-size clumps to show some degree of mismatch. However, this mismatch may alternatively be an indication of different hierarchical landscape structure at medium to large scales between the three ecoregions. The three avifauna lists are derived from three different ecoregions (Amherst - Northeastern Highlands; Austin - Texas Blackland Prairies and Central Texas Plateau; and Vancouver - Puget Lowland [Omernik] 1987). The mismatch of body-size clumps within this medium to large size range could be caused by different processes in each ecoregion producing a unique frequency distribution of landscape objects at medium to large scales (e.g., patches of trees). What actual structural difference (in terms of the spatial geometry) exists at medium to large scales is difficult to say, but this analysis indicates where researchers can begin to look. A detailed analysis of structure relevant to medium to large birds of each ecoregion may reveal some landscape features that are present in one ecoregion but absent in another. For example, if one knew the scale(s) at which medium to large birds respond to landscape structure, then the spatial distribution of the vegetation (relevant to birds in their respective ecoregions) could be compared between the two regions. This type of study may not only reveal structural differences between different landscapes, but may shed light on what types of processes are unique to different regions.

Each body-size clump, though, does not represent a group of species that respond to only landscape structure at one hierarchical level. I propose that birds in each body-size category respond to objects produced at several different hierarchical levels. For example, a small wren not only searches for prey items among fine textured objects at small scales (e.g., leaves and twigs), but it also establishes a home range based on large texture objects at large scales (e.g., tree and plant densities). However, the size of an organism dictates the size range of objects that it responds to in a landscape; small birds encounter landscape structure within smaller scale ranges than do larger birds. Small birds use objects at a scale range from millimeters when foraging for food (e.g., deciduous litter or pine needles) to kilometers when selecting territories (e.g., small areas of forest) whereas large birds use objects in a range from tens of centimeters (e.g., tree crown volume) to thousands of kilometers (e.g., a large forest tract) for the same choices. Thus, hypothetically, each body-size clump represents a group of species that respond to landscape structure within the same scale range, but some degree of overlap must exist when species in different clumps are sampling objects in a landscape.

But how can landscape structure, over evolutionary time, influence the size of an organism? An animal's size presents it with a trade-off between its ambit (or distance it can travel) and the size of objects that it samples. On the one hand, in a textured environment, smaller animals are exposed to more resources per unit area and do not have to travel long distances to obtain sufficient resources. Larger animals, though, are exposed to less resources per unit area because of the coarse grain of their choices; they gather enough resources by their ability to travel greater distances. Therefore, each body-size clump theoretically represents sizes of animals that satisfy this trade-off between the sizes of landscape objects available to an animal and how far an animal can travel to obtain resources (Holling 1992b).

As indicated earlier, though, birds sample landscape objects through a range of scales. At what scale is the distribution of landscape objects playing a dominant role in determining (over evolutionary time) the body-size of a bird? Most likely, the spatial distribution of landscape objects at large scales determines the body size of a bird (e.g., home range area). Although birds are sampling objects at smaller scales, these smaller objects are contained within objects at larger scales. For example, tree branches and leaves (small scales) that arboreal birds forage in are contained within patches of forest (large scales). The spatial distribution of forest patches probably dictates which sizes of birds are in a landscape because these patches contain all of the necessary structure for foraging, nesting, and protection from predators.

But what ultimately causes the gaps to appear in a body-size distribution? Theoretically, hierarchically structured landscapes produce a discontinuous frequency distribution of object sizes in an environment (Holling 1992b). The gaps that do occur in body-size distributions could be a result of two mechanisms. First, the gaps could represent "zones of exclusion" where animal sizes that are in these gaps are maladaptive in exploiting objects of either the upper or lower range of scales (Holling 1992b). Animals with body sizes that fall in these gaps are not able to satisfy the trade-off between the sizes of landscape objects available to it and how far it can travel to obtain resources. Second, the gaps could occur because animal sizes are "clustering" around the abundance of certain sizes of resources in an environment. These two mechanisms may not be mutually exclusive, both mechanisms combined could cause gaps to appear in animal body-size distributions.

Addressing the "zones of exclusion" hypothesis, gaps in body-size distributions may represent size ranges where birds are at a selective disadvantage. In some cases, the gaps between body-size clumps sometimes span only a few grams. Do a few grams really make that much of a difference to cause birds that lie in these gaps to be at a selective disadvantage? It probably does, especially during "ecological crunches" or perhaps under disruptive selection. Studies have shown that variation in morphological characters permit organisms to exploit different resources in a landscape (e.g., Lack 1971, Karr and James 1975, Fitzpatrick 1985, Grant 1986). In some cases, minute differences in morphological characters within or between species can result in some individuals having greater reproductive success than others. One example of this was in a study on "beak size" of an African finch in Cameroon, West Africa (Smith 1987, Smith 1990). It was demonstrated that lower bill width was bimodal for juvenile finches; the mean at one peak was 12.7 mm and the other peak was 15.7 mm. The abundance of soft- and hard sedge seeds, which are scarce during the dry season, was proposed to cause the selection for bimodality in bill sizes. Those finches that had extreme or intermediate bill sizes between the two peaks had a lower survivorship than birds with beak sizes near the peaks. It was hypothesized that this differential survivorship was due to feeding efficiency. Finches with large bills could feed efficiently on the hard seeds and finches with small bills could feed efficiently on the soft seeds (Smith 1987, Smith 1990). Along these lines, body sizes that lie in the gaps may not be able to obtain resources efficiently, and this may cause the clumps to appear in size distributions.

I propose that the 10 body-size clumps determined in this study represent suites of species that respond to similar sizes of objects in a landscape within the same range of scales. These landscape objects may be of similar sizes, but they can be qualitatively different. A wide variety of objects can be found at each hierarchical level in a landscape, and birds have developed a wide variety of natural life history strategies to exploit all objects at all scales. For example, an arboreal bird species exploits tree needles and leaves (small-scale objects), large trees (medium-scale objects), and patches of trees (large-scale objects). A similar-sized ground bird species exploits grasses (small-scale objects), small patches of grasses (medium-scale objects), and large meadows (large-scale objects). Both birds are measuring the same sizes of objects at each scale, but the objects are qualitatively different. The quantity of scale-dependent landscape objects (specific to each species) dictates the presence or absence of a species in a given area. If the sizes of objects utilized by species in one body-size clump were known, these sizes are probably relevant to all species that fall in this size category. If body-size clumps represent groups of species that respond to landscape structure within the same range of scales, then the 10 body-size clumps found in this study sets the stage for exploring the sizes of objects (within a particular scale range) of a wide variety of species.

Quantity of Species in Each Clump

In this chapter, several of the different ecoregions differed with respect to the number of species in certain body-size clumps. Recall that I hypothesized that the number of species in each clump represents the diversity of resources within a particular scale range.

It was predicted that the Tucson and Austin avifauna lists would have the fewest number of small birds. Indeed, the Tucson region (of the desert biome) had the fewest number of small-sized species (category 2) than any of the other temperate forest regions. One interpretation of this disparity is that the interaction of structuring processes in the temperate forest regions produced a greater diversity of structures (e.g., more tree species) available for category 2 birds. The fewer number of category 2 birds in the Tucson area may be a result of the limited amount of fine textures in deserts when compared to forests. The vertical height diversity in deserts is limited, most of the fine texture is distributed over a layer just above the ground. In contrast, the large volume of canopy cover in the forested ecosystems would contain a diversity of fine-texture resources exploitable by birds, theoretically resulting in more category 2 birds in temperate forests than in deserts. The Austin avifauna list also had a smaller number of species in category 2 than the other temperate forest ecoregions (not significant though). Austin is located in Texas Blackland Prairies and Central Texas Plateau (Omernik 1987), and this ecoregion has less rainfall and more sparsely distributed vegetation than the other temperate forest ecoregions (Bailey 1995). A decreased amount of rainfall and open stands of trees would result in a decreased amount of fine landscape texture (e.g., tree crown volume) that small birds could exploit.

For category 5 birds, the Tucson region (of the desert biome) had more species than any of the other ecoregions in the temperate forest biome (although only significant between the Seattle/Vancouver and Tucson comparison). The greater amount of category 5 birds in the Tucson region is more difficult to explain. One would think that forests would have more resources than deserts even at medium scale ranges. However, deserts have much more open areas than forests; the combination of open ground cover and of scattered vegetation patches may provide more types of resources for category 5 birds. Many of Tucson's category 5 birds are ground foragers or hunt in open areas (e.g., Pyrrhuloxia, Elf Owl, Canyon Towhee, Abert's Towhee, and Inca Dove) (Ehrlich et al. 1988). A combination of open ground and patches of trees or bushes is used by many birds in this size category. Perhaps at scales relevant to category 5 birds, the landscape mosaic of temperate forest ecoregions provides limited opportunities. It would be interesting to see if this pattern holds true for other desert and temperate avian communities on other continents.

Revisiting Body-size Clump Patterns & Future Research

The results in this study are consistent with the hypothesis that body-size clumps reflect both the qualitative and quantitative properties of hierarchically structured landscapes. However, this type of study does not lend itself to the traditional experimental approach where variables are manipulated to understand the underlying mechanisms that explain a given pattern. Typically, the experimental approach is only applicable to ecological questions at small scales that enable the researcher to tightly design an experiment. This type of approach is not practical for testing clump theory; testing of this theory lies under the construct of confirmation. Confirmation uses multiple lines of evidence to confirm or reject the generality of a theory (Pickett et al. 1994). Confirmation of a theory inherently requires a variety of empirical cases that support the claims of a theory. So far, the empirical patterns detected in this study are generally consistent with the expectations of clump theory (although the Amherst vs. Tucson comparison does not). However, many more independent examples are needed to determine whether body-size clumps truly reflect the hierarchical structure of landscapes. Such studies are currently underway in the lab of C. S. Holling.

A hierarchical framework has a wide application to studying many important aspects of ecology, such as optimal foraging theory, habitat selection, population dynamics, and the impact of habitat fragmentation on animal communities (Kotliar and Wiens 1990). At this stage, it appears that body-size clumps may be useful as a tool to explore both the hierarchical structures of landscapes and at what scales animals respond to structure over a range of scales. The important theoretical concepts of this technique for researchers are (1) that body-size clumps reflect the unique hierarchical structure of a landscape, (2) that birds in each body-size clump respond to similar sizes of landscape objects within the same range of scales, and (3) that the number of bird species in a clump reflect the diversity of resources within a scale range.

Understanding how changes in the landscape affect the distribution and abundance of animal populations is an important issue in ecology (e.g., Levin 1992, Gardner et al. 1993, Rahel 1990, Kotliar and Wiens 1990). Many cross-scale studies have shown that landscape heterogeneity and patchiness can be found at almost any scale (Powell 1989, Levin 1992). Ecologists have developed different techniques and models that attempt to capture and describe patterns in ecological systems (Gardner et al. 1987, Milne 1988, Fahrig 1988). Some of these techniques have been used to determine the hierarchical structure of landscapes. For example, fractal analyses have been highly regarded as a tool in ecology to describe landscapes and landscape changes across a variety of scales (Milne 1988, Mandelbrot 1977, Bradbury and Reichelt 1983). In a hierarchical analysis, fractal breaks are hypothesized to represent the transitions from one hierarchical level to another (e.g., Milne 1988). These analyses, though, are based on how we measure the landscape and not whether animals measure hierarchical structure in landscapes.

Using animal body-size clumps removes the subjectivity that inevitably occurs when humans measure landscape structure at different scales. Although our eye tells us that the landscape structure is quite different from one ecosystem to the next (or from one scale to the next), the landscape differences that we perceive (or measure) may be quite different than what animals "perceive". For example, the Tucson avian community (desert biome) had more category 5 birds than avian communities of the temperate forest biome. This indicates that desert regions may have more resources for category 5 birds than temperate forest regions. Intuitively, one would have hypothesized that temperate forest landscapes would have more resources (at any scale) because these ecosystems are much more structurally diverse than deserts.

If ecosystems were hierarchically structure, then the structure and function of ecosystems may be controlled by a small number of processes at different scales (Holling 1992b, O'Neill 1986). Each hierarchical level would be defined by its own spatial textures and set of processes. This would greatly simplify studying cross-scale dynamics of ecosystems. Particularly, it would simplify models that attempt to predict the behavior of ecosystems across space and time. Examples of such models include the spruce/budworm system of eastern North America (Clark and Holling 1979) and the Everglades system of Florida (Walters et al. 1992). Body-size clumps may provide additional evidence of the hierarchical organization in ecosystems. Further, body-size clumps may help researchers to relate scale-dependent landscape structure to the different species in a community; this has been an elusive problem to solve in ecology (Levin 1992, Kotliar and Wiens 1990). Body-size clumps will greatly simplify this endeavor because theoretically the species in each body-size clump respond to structure within the same range of scales.

The proposed 10 body-size clump model represents groups of birds that theoretically respond to similar sizes of landscape objects within the same range of scales. The next step is to relate the body-size clump structure to actual scale-dependent landscape structure. But how does one determine what range of scales and sizes of landscape objects are relevant to species in each body-size clump? I address this question in chapter 4 by correlating the counts of birds in each clump to the amount of tree canopy cover remaining (at different scales) in suburban areas mentioned in this study. Fragmentation of suburban habitats affects a variety of species, but different sizes of animals respond to different scales of fragmentation. For example, in suburban habitats, a wren probably would respond to the amount of small trees and shrubs in your backyard, but a hawk would respond to the distribution of trees in your whole neighborhood. Knowing the scale-dependent objects important to birds in each body-size clump would greatly enhance our understanding of how human-modified landscapes affect avian communities.

An additional question is whether the 10 body-size clump model truly represents the unique hierarchical signature of temperate forest landscapes. This model was chosen even though a few other models gave a significant match. Also, this model may be a result of the large degree of species overlap between the temperate forest avifauna lists. If the 10 body-size clump model truly represented the hierarchical structure of the temperate forest biome, then a comparison of temperate forest avian communities of two different continents should reveal the same clumps. In chapter 3, I compare the body-size clumps of the temperate avian communities of North America and Europe. If the 10 body-size clump model reflects the hierarchical structure of temperate forest landscapes, then the avian clump structure of New World and Old World temperate forest biome should match.

Summary

Most of the results were consistent with the predictions that were derived from the textural-discontinuity hypothesis. The temperate forest avifauna comparisons did show matching in the location of their clumps whereas two of the three desert versus temperate forest comparisons did not match. The results in this chapter suggest that avian communities in temperate forest landscapes display roughly 10 body-size clumps. Further, within the smallest size range, the body-size clumps matched quite well across all avifauna lists, even between the Amherst and Tucson lists that represented drastically different landscapes. This may indicate that structure at small scales is geometrically similar across all types of landscapes. In terms of the quantity of species in each clump, the avifauna lists from landscapes with theoretically more fine-textured resources had more small-sized species. In addition, the Tucson avifauna (desert landscape) had more category 5 birds than the other temperate forest avifauna; perhaps a combination of more open areas with patches of vegetation provide more resources for larger birds.

The above findings are at least consistent with the hypothesis that avian body-size clumps seem to reflect both qualitative and quantitative aspects of the hierarchical structure of landscapes. This would be extremely useful for ecologists studying how scale-dependent changes in a landscape affect the distribution and abundance of animal populations. For example, the loss of species in a certain body-size clump would indicate at what scale humans have altered the landscape (of course one has to determine the scale at which birds respond to structure). Detecting the hierarchical structure of landscapes with body-size clumps is unlike previous ecological techniques (e.g., fractal analysis) that measure landscape structure at different scales. This is an important distinction between the two techniques because the way animals measure discontinuous landscape structure may be completely different than the way ecologists measure them. Although the results were consistent with the textural-discontinuity hypothesis, more tests are needed to become more confident that animal body-size clumps reflect the hierarchical structure of landscapes.

CHAPTER 3

BODY-SIZE CLUMPS OF NEW WORLD AND OLD WORLD AVIAN COMMUNITIES

Introduction

Body-size clumps are hypothesized to reflect the hierarchical structure of landscapes. Where the clumps appear in a body-size distribution theoretically reflects the unique hierarchical structure of a landscape, and the number of species in each clump reflects the diversity of resources available to species in each clump at a limited range of scales (Holling 1992b). This was formally stated as the *textural-discontinuity hypothesis* (Holling 1992b). Testing this hypothesis, Holling (1992b) found that the bird fauna of the boreal forest, of the short-grass prairie, and pelagic birds of the pacific northwest were grouped into several distinct body-size clumps. The avifauna lists were dissimilar in terms of the number of species in each clump and where the clumps were located in a size distribution. The differences seem to reflect qualitative and quantitative differences in the physical architecture in each ecosystem. These initial analyses revealed that body-size clumps may reflect an ecosystem's unique hierarchical landscape structure, but only a few data sets were analyzed and additional tests are needed.

In chapter 2, several bird faunal lists of North America were used to determine whether body-size clumps exist. Ten body-size clumps were proposed to reflect the hierarchical landscape structure of the temperate forest. However, about 50% overlap in bird species occurred among the data sets that were compared. Thus, there is a possibility that the body-size clumps may, in part, be determined by the phylogenetic similarity of the faunal lists. Further, this was only one example, and additional tests are needed. Thus, an independent analysis should be conducted between avifauna lists that share very few species. A good comparison would be between eastern North American and European avian communities because very little species and genera overlap occur between the two continents (Helle and Monkkonen 1990). For example, eastern North America and Europe do not have many bird genera in common for birds that winter south of U.S. and Europe (Monkkonen and Welsh 1994). If body-size clumps reflect the hierarchical structures of landscapes, then the edges of body-size clumps should match between North American and European avian communities of the same biome. Such a comparison further tests the textural-discontinuity hypothesis.

Historically, though, the landscape patterns of North American and European continents have been quite different. In Europe, landscapes were much more fragmented than landscapes in North America. European forests were almost completely fragmented (e.g., Kurten 1972) because of Pleistocene glaciations in the Old World. Most of Western and Central Europe were covered by some type of tundra (Peterson et al. 1979), and forests persisted in small fragments along European mountains in the south (Huntley 1993) with a few small remnants in the north. In contrast, North American Pleistocene glaciations did not result in extensive fragmentation (Monkkonen and Welsh 1994). Glaciation shifted the north to south boundaries of temperate and boreal regions, but extensive deciduous and coniferous forests existed south of the glaciers (CLIMAP 1976, Webb 1988, Pielou 1991). Thus, European forests during the Pleistocene were quite fragmented whereas North American forests were quite extensive and continuous.

In addition, after the Pleistocene glaciations, the scale of human impact was much larger and happened much earlier in Europe than in North America. Humans in the Old World had developed an advanced form of agriculture, domesticated much of our barnyard animals, and built many cities long before peoples of the New World did so (Crosby 1986). Major landscape changes in temperate regions of Europe began to take place 5000 years ago with much of the landscape being converted into cultivated areas (Chambers 1993). It has been estimated that present European temperate landscapes already existed 1000 years ago in certain parts of Europe (Rackman 1980, Thirgood 1981). In eastern North America, large scale human impact of temperate regions did not begin until 300 years ago with greatest changes occurring within the past 100 years (Williams 1989). Within the boreal zone, human impact occurred much more recently in both continents, but European regions were impacted much earlier than North American regions (Monkkonen and Welsh 1994). For example, large scale forest harvesting occurred in Finland between 1500 and 1900 (Darby 1956), but large scale forest clearing did not begin in the Canadian boreal forest until the 1950s.

Fragmented European forests limited the amount of area available to forest taxa, ultimately decreasing the diversity of European forest flora (see Huntley 1993). Also, fragmented forests are characterized by a patchy distribution of forested areas. I hypothesize that fragmentation may primarily reduce the diversity of resources that could be exploited by medium-sized birds than small or large birds. Small birds theoretically could still find sufficient resources within each small patch of forest because their small size exposes them to more resources per unit area than larger birds. Also, large birds could find sufficient resources in a fragmented landscape because their ambit is large enough to travel between patches. However, medium-sized birds could neither find enough resources in each small patch nor travel between the patches. If body-size clumps reflect landscape structure, then fewer clumps within certain size ranges would indicate a limited diversity of resources at certain scales. Because of the greater extent of European forest fragmentation, I hypothesize that there would be fewer body-size clumps in the medium size range of the eastern European avifauna list than of the North American avifauna list.

Furthermore, the negative effects of fragmented European forests on medium-sized birds would ultimately decrease the number of medium-sized European species. It was hypothesized that the number of medium-sized species would be dramatically less in Europe than in eastern North America. Fragmentation of forested landscapes would also cause less fine textured resources to be available to small birds because of decreased diversity of forest taxa. Remnant fragments, theoretically, could support small birds but the diversity of forest taxa would be reduced. Thus, I hypothesize that the number of small species would be less in Europe than in eastern North America.

To test the above predictions, I compared eastern North American and European body-size distributions of avian communities from the boreal and temperate forest biomes. All of the above predictions were based on the hypothesis that body-size clumps reflect both quantitative and qualitative properties of hierarchically structured landscapes The main objectives were 1) to determine whether the avian body-size clumps of the same biome matched between the two continents, 2) to determine whether the number of birds in each body-size clump differed between the two continents, and 3) to determine whether the number of clumps differed between the avifauna lists of the two continents. A fourth objective was to compare the avian body-size clumps between the two biomes (temperate and boreal) on the same continent. I hypothesize that the body-size clumps within a small body-size range would display a better match than a larger size range. This hypothesis was based on results of chapter 2 that showed the best match occurred within the small body-size range between avifauna of the desert and temperate forest biome.

Methods

The first step was to determine the geographic boundaries for the temperate and boreal biomes on both continents. These boundaries were derived from Odum's (1971) map of the major biomes of the world and are displayed in Figures 3-1 and 3-2. The next step was to construct avifauna lists of each continental biome.

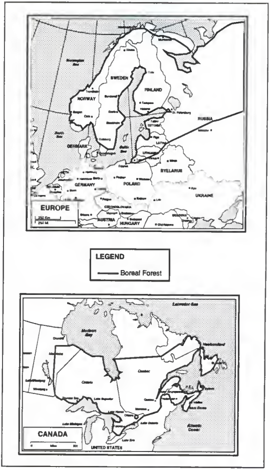


Figure 3-1. Outline of the boreal forest biome in eastern North America and Europe.

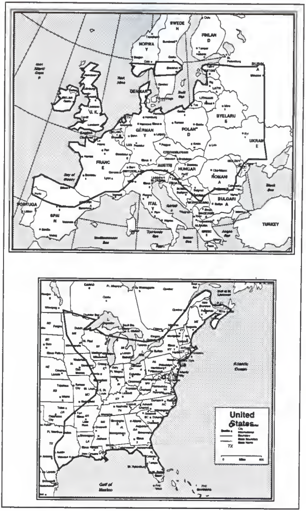


Figure 3-2. Outline of the temperate forest biome in eastern North America and Europe.

These avifauna lists consisted of all landbirds, excluding exotics in each respective continent, with breeding ranges overlapping the geographic boundary of the temperate and boreal biome. Breeding ranges of European birds were determined from Jim Flegg's field guide (1990) whereas breeding ranges of eastern North American birds were determined from the Peterson Field Guide (1980). All bird masses (in grams) were derived from Dunning's (1992) book of avian body masses; for each species, the mass used was the mean mass of both reported male and female averages. Some of the breeding ranges of certain species barely overlapped with the chosen geographical regions of eastern North America and Europe. In these cases, the field guides were consulted to ascertain which type of biome these birds normally breed in. For example, if a species had part of its breeding range in the boreal forest, but it was characterized as breeding in the tundra, this species was not included in the boreal forest bird list.

The body-size clumps of eastern North American and European avian communities (boreal and temperate zones) were determined as outlined in the methods section of chapter 2. Avifauna lists of eastern North American boreal and temperate biomes were compared to their respective European avifauna lists. Only body-size clumps that gave a significant match (alpha = 0.05) and had the most equitable number of clumps between the lists were considered as the body-size clump pattern representing each biome.

If one body-size clump model was determined for the boreal and temperate avifauna lists of each continent, the clumps were then compared within each biome between the continents and between each biome within a continent. The purpose of this comparison was to determine whether body-size clumps of each biome showed similar trends in terms of the number of clumps and the number of species within certain size ranges.

Between Continents

Because European landscapes have been more fragmented than eastern North American landscapes, I predicted that temperate and boreal eastern North American avifauna lists would display more body-size clumps than European avifauna lists. These additional clumps would appear in the medium size range because the relatively unfragmented eastern North American forests provide a greater diversity of landscape resources that could be exploited by medium-sized birds. In addition, the body-size clumps of the temperate eastern North American avifauna lists should closely match the clumps determined for the temperate forest biome of chapter 2.

The increased amount of fragmentation in Europe would also affect the number of species within certain size ranges. I predicted that European avifauna lists would contain dramatically fewer medium-sized birds than eastern North American avifauna lists. This is because medium-sized birds (especially forest species) would not be able to obtain enough resources in fragmented European landscapes. European avifauna lists were also predicted to have fewer small-sized birds than eastern North American avifauna lists. Fragmented European landscapes would contain less fine textured resources (due to decreased forest taxa diversity) than eastern North

American landscapes. G-tests (alpha=0.05) were used to detect differences in the number of species in each clump between the biomes.

Within Continents

Because fine textured resources are hypothesized to be geometrically similar between different landscape types, I hypothesized that body-size clumps within a small size range (around 1.3 log g and below) would be similar between the temperate and boreal biomes on each continent. The clumps within this small size range would be more similar than larger size ranges. This size range was chosen because body-size clumps lined-up within this size range between different landscapes of North America (chapter 2).

Results

The avifauna lists for the eastern North American and European temperate and boreal biome are displayed in Appendix B and C. Less than 10% species overlap occurred between North American and European avifauna lists (both biomes). Below, the results of the avifauna clump analysis are given.

Between Continents

Temperate forest biome. The Gap Rarity Index found 9 clumps in the eastern North American avifauna and 7 clumps in the European avifauna. Match analyses (7 to 15 clumps) of the two temperate forest avian communities resulted in only one significant match ($P < 0.05$) with 10 body-size clumps in eastern North America and 7 body-size clumps in Europe (Figure 3-3). The body-size clump pattern in eastern North America had 3 extra clumps between 16.0 g and 52.0 g (1.2 log g and 1.7 log g: Figure 3-3). The body-size clumps defined by the upper and lower masses are shown in Table 3-1. These body-size clumps are similar to the body-size clumps of temperate forest ecoregions discovered in Chapter 2 (Table 3-2).

The number of species in certain size ranges for the two continents is displayed in Table 3-1. Within the smaller size range of 7.0 g - 32.7 g, eastern North America had more species than Europe (91 vs. 84), but this was not significant ($P > 0.05$); within the medium size range of 32.8 g - 105.0 g, eastern North America had more species than Europe (43 vs. 27), but this was not significant at conventional levels ($P = 0.055$); and within the large size range of 105.1 - 2085.0 g, Europe had more species than eastern North America (51 vs. 43) but this was not significant ($P > 0.05$).

Boreal forest biome. The Gap Rarity Index found 8 clumps for both the eastern North American and European avifauna lists. Match analyses (8 to 15 clumps) of boreal forest avian communities resulted in several significant matches ($P < 0.05$): comparing eastern North America vs. Europe, 10 vs. 9, 13 vs. 9, 14 vs. 9, and 15 vs. 9 models were found to be significant. Of these models, the 10 vs. 9 model was chosen to represent the landscape structure of the boreal forest biome because it had the most equitable number of clumps (Figure 3-4). Using this 10-9 model, eastern N. America had 1 extra clump between 27.4 g and 39.6 g (1.4 log g and 1.6 log g: Figure 3-4).

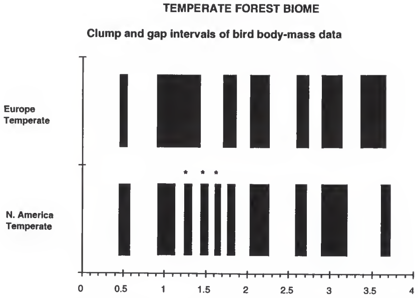


Figure 3-3. Avian body-size clump structure of the eastern North American and the European temperate forest biome. North American body-size clump structure has 10 clumps and the European body-size clump structure has 7 clumps. The asterisks indicate 3 extra clumps in the North American body-size clump structure between 1.2 and 1.7 log grams.

Table 3-1. The size ranges of European and eastern North American temperate forest avian body-size clumps. The number of species in each clump is also listed.

Europe		Eastern North America	
Size range(g)	# of species	Size range (g)	# of species
0.0 - 6.9	2	0.0 - 6.9	5
7.0 - 32.7	84	7.0 - 16.2	56
		16.3 - 21.5	16
		21.6 - 32.7	19
32.8 - 102.0	27	32.8 - 52.0	20
		52.1 - 105.0	23
103.0 - 188.0	16	105.1 - 186.0	11
189.0 - 570.0	22	187.1 - 576.5	18
571.0 - 2080	13	577.0 - 2080.5	14
> 2080.0	5	> 2080.5	2

Table 3-2. The size ranges of temperate forest avian body-size clumps determined from Amherst, Austin, and Vancouver avifauna lists (Chapter 2) compared to those from eastern North American temperate forest avifauna lists (this chapter).

Amherst, Austin, Vancouver regions Size range (g)	Eastern North America Size range (g)
0.0 - 6.9	0.0 - 6.9
7.0 - 16.5	7.0 - 16.2
16.6 - 21.6	16.3 - 21.5
21.7 - 33.75	21.6 - 32.7
33.76 - 61.6	32.8 - 52.0
61.7 - 115.0	52.1 - 105.0
115.0 - 184.0	105.1 - 186.0
185.0 - 576.5	187.1 - 576.5
577.0 - 2080.5	577.0 - 2080.5
> 2080.5	> 2080.5

The body-size clumps defined by the upper and lower masses are shown in Table 3-3.

Body-size clumps defined by the upper and lower masses of each clump resulted in slightly different size ranges between the two continents (Table 3-3). Thus, to compare continental differences in the number of species within each body-size clump, I arbitrarily used the European size ranges. Within the smaller size range of 7.0 g - 33.5 g, eastern North America had more species than Europe (71 vs. 56), but this was not significant ($P > 0.05$); within the medium size range of 33.6 g - 82.3 g, eastern North America had significantly more species than Europe (25 vs. 13, $P < 0.05$); and within the large size range of 82.4 g - 2204.0 g, Europe had significantly more species than eastern North America (46 vs. 29, , $P < 0.05$).

Within Each Continent

Looking at each continent separately, the body-size clumps of the temperate and boreal biome matched within smaller and larger size ranges. However, the medium size range (16.3 g - 316.0 g; 1.2 log g and 2.5 log g) had the most mismatch (Figure 3-5).

Trends in Body-size Clump Distributions

Here, the results are summarized in terms of whether both the temperate forest and boreal biome showed some similar trends in the results mentioned previously.

Between the two continents. First, both eastern North American biomes had more species in the smaller size range (around 7.0 g to 33.0 g) and the medium size range (temperate forest: 34.0 g

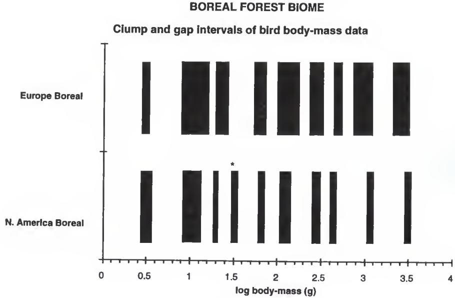


Figure 3-4. Avian body-size clump structure of the eastern North American and the European boreal forest biome. North American body-size clump structure has 10 clumps and the European body-size clump structure has 9 clumps. The asterisk indicates 1 extra clump in the North American body-size clump structure between 1.4 and 1.6 log grams.

Table 3-3. The size ranges of European and eastern North American boreal forest avian body-size clumps. The number of species in each clump is also listed.

Europe		Eastern North America	
Size range (g)	# of species	Size range (g)	# of species
0.0 - 6.9	1	0.0 - 6.9	4
7.0 - 16.6	31	7.0 - 15.2	39
16.7 - 33.5	25	15.3 - 27.3	23
33.6 - 82.3	13	27.4 - 39.6	15
		39.7 - 89.0	22
82.4 - 185.0	15	89.1 - 185.5	11
186.0 - 365.0	11	186.0 - 365.0	3
366.0 - 570.0	8	366.0 - 577.0	8
571.0 - 2204.0	12	578.0 - 2354.5	6
> 2204.0	4	> 23545.0	2

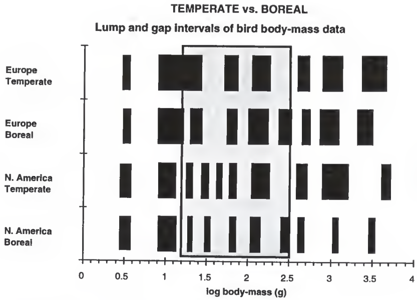


Figure 3-5. Avian body-size clump structure of the eastern North American and the European boreal and temperate forest biome. The box ☐ outlines a size range (log 1.2 g and 2.5 g) with the most mismatch between the temperate and boreal zones on each continent.

to 105.0 g; boreal forest: 34.0 g to 82.0 g) than their respective European biomes. However, in the larger size range (temperate forest: around 105.0 g - 2080.0 g; boreal forest: around 82.4 g - 2204.0 g) fewer species occurred in both of the eastern North America biomes than in Europe. Second, more body-size clumps occurred in eastern North America than in Europe for both biomes. The additional clumps appeared in the size range of 16.0 g - 52.0 g (1.2 log g and 1.7 log g: Figures 3-3 and 3-4).

Within each continent. On both continents, most of the mismatch between the biomes occurred in the medium size range (16.3 g - 316.0 g; 1.2 log g and 2.5 log g) (Figure 3-5).

Discussion

Many new insights about the hierarchical landscape structure of eastern North American and European temperate and boreal biome were revealed by the clump analyses. In the following discussion, I will (1) discuss the similarities and differences between eastern North American and European avian body-size clumps, both in terms of the number of clumps and the number of species within certain size ranges, and (2) discuss the similarities and differences between temperate and boreal avian body-size clumps on the same continent in terms of the number of clumps within certain size ranges.

Cross Continental Body-size Clump Comparison

How well did they match? The temperate and boreal forest avian body-size clumps between eastern North America and Europe both showed significant matches. New World and Old World avifauna lists (from the same biome) had very little species or genera overlap, but they had similar body-size clump structures. This is evidence that body-size clump matches are not due to species overlap. I propose that structuring processes in the temperate forest biome produce a hierarchical landscape structure that is consistent from one continent to the next. Essentially, over evolutionary time, this hierarchical landscape structure is a "template" that is favorable for only certain animal body sizes. Holling (1992b) proposed that body-size clumps could be used to reflect existing hierarchical structure of landscapes, and results from this study do not refute this idea. In addition, the 10 temperate forest body-size clumps of eastern North America in this study matched quite well with the 10 body-size clumps of temperate forest regions of North America shown in Chapter 2. As mentioned previously, birds in each body-size clump are theoretically responding to structure within the same range of scales. If true, this match sets the stage to explore whether birds in each clump respond to landscape structure within the same range of scales.

Although body-size clumps matched between the two continents, more clumps occurred in the medium size range in both temperate and boreal biomes of eastern North America than of

Europe. The temperate forest biome of eastern North America had 3 extra clumps between 16.0 g and 52.0 g, and using the 10 vs. 9 model, the boreal forest biome of eastern North America had one extra clump between 27.4 g and 39.6 g. These additional clumps could be a result of the unique histories on these two continents. As mentioned before, European forests (since the Pleistocene) have been quite fragmented whereas North American forests have been relatively extensive and continuous (Monkkonen and Welsh 1994). This fragmentation difference between the two continents led to marked differences in the floral diversity. In the temperate zone, several studies have reported the low taxonomic diversity of European forest flora, compared to North American flora (Kurten 1972, Sauer 1988). Many of the forest taxa became extinct in Europe during the Pleistocene glaciations, and Huntley (1993) proposed that the low taxonomic diversity of European forests was primarily due to the limited amount of area available to forest taxa. The continuous forest tracts of North America may have provided more diverse landscape resources that could be exploited by medium-sized birds. The additional clumps in eastern North America possibly reflect these additional resources in N. American landscapes.

However, the relatively continuous forest tracts of North America should provide more types of resources for all sizes of birds. Why were there not additional clumps in the eastern North American small and large size ranges when compared to the European small and large size ranges? Probably, the hierarchical landscape structure at small and large scales was preserved in European landscapes, despite the high degree of forest fragmentation. Most likely, the *diversity* of resources at small and large scales had been changed; this would primarily affect the quantity of species at small and large size ranges (see section below), not the position or the number of clumps within these size ranges. At scales pertinent to medium-sized birds, the landscape structure (e.g., forest cover) probably changed the most. As landscapes become fragmented, I suggest that medium-sized species theoretically would not be able to find enough resources within remnant patches of forest nor could they travel between patches. Thus, many forest patches may not be available to medium-sized birds in fragmented landscapes.

Quantity of species in each body-size clump. In both the temperate and boreal biomes respectively, eastern North America (compared to Europe) had more species in the medium size range. This difference was significant for the boreal biome, but not significant for the temperate biome at conventional statistical levels. One explanation for this is that a greater diversity of resources is available to medium-sized animals in eastern North America than in Europe. The high degree of fragmentation in Europe left a number of forest patches separated by some distance from one patch to the next. Fragmentation probably selected against European medium-sized animals because they could neither acquire enough resources within each patch nor, because of their ambit, could they travel between patches to gather enough resources.

This explanation is similar to what Morton (1990) proposed as the mechanism of extinction of many middle-sized Australian mammals. Changed fire regimes and the introduction of rabbits caused the distribution of productive patches to become steadily smaller and to be spaced steadily farther apart. Small animals could still find enough resources in the remaining small patches whereas large animals had an ambit large enough to travel between the patches. Middle-sized animals went extinct because they could neither find enough resources in each small patch nor travel between patches. A similar scenario may have happened to medium-sized European birds since the Pleistocene.

In the smaller size range, the slightly larger number of eastern North American than European birds could also be attributed to the greater amount of fragmentation in Europe than in eastern North America. As mentioned earlier, the fragmented forests of Europe have a low taxonomic diversity of forest flora due to limited amount of areas available to forest taxa (Huntley 1993). Limited forest cover also means decreased vertical height diversity across European landscapes. Perhaps these two factors reduced the number of smaller bird species that could specialize on forest vegetation in Europe. On the other hand, extensive forests in eastern North America may have provided more unique opportunities for small bird species to specialize on specific types of vegetation at small scales. This resulted in more small-sized species in North America.

It is interesting to note that eastern North America contains a large number of neotropical migrants whereas only a few long-distant migrants (that winter in Africa) occur in Europe (Monkkonen and Welsh 1994, Rappole 1995). Most of the European migrants are primarily early successional species whereas many N. American migrants are found most often in mature forest (Monkkonen and Helle 1989). These natural life history differences of eastern N.

American and European birds are an indication of how fragmented landscapes may affect the natural life history characteristics of birds. On possible explanation is that the extensive eastern North American forests (compared to the fragmented European forests) provided a greater amount of opportunities for small to medium sized birds to specialize on forest vegetation.

Finally, the greater number of European than eastern N. American birds in the larger size range may also be a result of the higher degree of fragmentation in Europe than in eastern North America. Perhaps large amounts of open areas, combined with patches of forest, are suitable for larger bird species. The species lists of both continents indicate that a majority of the larger birds are raptors (Appendix B and C). Raptors generally prefer to nest and forage in semi-open country (Ehrlich et al. 1988), and the fragmented European landscape historically had more semi-open areas than the landscape in eastern N. America. Perhaps a landscape mosaic that contains a combination of open areas with patches of vegetation (e.g., trees) provides more opportunities for large species than a landscape that is completely forested or open. Thus, fragmented European landscapes may have had more opportunities for large birds to specialize on different aspects of this landscape mosaic. This ultimately would allow for the presence of a greater number of European than eastern N. American large-sized species.

Both biomes showed that fewer small- and medium-sized birds and more large birds exist in Europe than in eastern North America. These results were consistent for both biomes, but the trends were not statistically significant (except for the boreal biome: medium-sized birds). Also, it should be noted that the trends found in this study could be explained by historical differences in landscape structure on the wintering grounds (e.g., South America and Africa). Perhaps the South American landscape provided more opportunities for the speciation of small to medium-sized migrants, and this is the reason for the increased number of birds in eastern North America than in Europe. To address whether fragmentation disproportionally affects small to medium-sized species, more comparisons are needed between fragmented and unfragmented forested landscapes. Multiple examples of the trends noted in this study will provide more confidence that these trends are real.

Nevertheless, the cross continental comparisons in this study suggest that eastern N. American birds in the small to medium size ranges (7.0 g - 105.0 g) are most susceptible to human-caused fragmentation of forested landscapes. The European body-size clumps, which consist of species that have experienced fragmentation for a long period of time, have fewer species in the medium and small size ranges than their eastern N. American counterpart. This suggests that if eastern North America became as fragmented as Europe, one would expect a dramatic population decline or extinction of small to medium sized bird species. This may already be happening in North America. Several eastern N. American breeding passerine populations are hypothesized to be declining (e.g., Whitcomb et al. 1981, Terborgh 1989, Rappole 1995, although see James et al. 1992) whereas most European passerine populations are not declining (Opdam et al. 1985, Haila 1986). Monkkonen and Welsh (1994) suggest that the evolutionary history of European passerines resulted in an avifauna that is adapted to fragmentation. European passerines are not sensitive to fragmentation because European landscapes have been fragmented for a long period of time. However, eastern N. American passerines have evolved in a botanically more diverse and extensively forested landscape, and some species (especially interior forest specialists) are particularly sensitive to fragmentation.

North American passerines that are hypothesized to be declining, such as the Wood Thrush (*Hylocichla mustelina*), Yellow-throated vireo (*Vireo flavifrons*), and Hooded Warbler (*Wilsonia citrina*), all have sizes that fall in the small to medium size range (7.0 g - 105.0 g). Fragmentation of the breeding grounds may be only one cause for the decline of some North American passerines, other causes include tropical deforestation and the habitat decline of stopover sites (Rappole 1995, Terborgh 1989, Hagan and Johnston 1992). All three causes probably play a role in the proposed decline of some species. The results in this chapter are consistent with the hypothesis that small to medium sized interior forest specialists will be most affected in the near future if fragmentation of North American breeding grounds reach proportions similar to Europe.

Within Continental Body-size Clump Comparison

As predicted, the avian body-size clumps of the boreal and temperate biome matched within the smaller size range (0.0 g - 16.3 g). However, the body-size clumps at the larger size range (> 185.0 g) also matched. The medium size range (16.3 g - 185.0 g) had the most mismatch when body-size clumps of temperate and boreal biomes were compared to each other on the same continent. This suggests that landscape structure at small and large scales is similar between boreal and temperate zones, but structure at medium scales is different between the two biomes. This of course depends on whether the position of clumps at the medium size ranges is a true reflection of the hierarchical structure in each biome. But why is there a mismatch between clumps in the medium size range and a match at the smaller and the larger size range?

Most likely, mesoscale disturbance processes would have the most appreciable effect on animal body-size clumps. Many mesoscale disturbances alter the spatial distribution of resources at scales relevant to most organisms. For example, mesoscale disturbance processes, such as fires, insect outbreaks, storm damage and diseases, alter the spatial distribution and abundance of trees and plants at a scale from 0.03 - 100.0 km (Holling 1992b) If clumps reflect structure in landscapes, then landscapes with different disturbance regimes should show some differences in body-size clump patterns. This probably will not occur at all scales. Where body-size clumps match between different landscapes would indicate the range of scales where structure is geometrically similar. Where there is a mismatch would be an indication of the range of scales where landscape structure is geometrically different.

Thus, the match of boreal and temperate avian body-size clumps at the small and large size ranges and the mismatch at the medium size range suggests that structure is similar at small and large scales but different at middle scales. Boreal and temperate mesoscale processes may produce geometrically different types of structure relevant to medium-sized birds, but similar structure relevant to small and large birds. One possible mesoscale process that affects landscape structure at scales relevant to avian communities is fire. Differences in the boreal and temperate fire regime may explain the apparent mismatch in the avian clump structure (at the medium size range) between the two biomes. In the boreal forest, the fire regime burns a site approximately every 50 to 100 years (Heinselman 1973, Zackrisson 1977), and each fire typically burns hundreds of thousands of square kilometers (Wein and MacLean 1983). In contrast, the fire regime of deciduous forests rarely burn at such a large scale; most of the disturbance in temperate forests is controlled by single and multiple treefalls (Oliver and Stephens 1977). As a result, the age structure of deciduous forests is uneven whereas large tracts of boreal forest tend to be even aged (Cayford and McRae 1983). In part, the different fire regimes cause structural differences between temperate and boreal forests (another possible disturbance includes insect outbreaks - see Holling 1992a). Temperate forests consist of a variety of patches with different tree species whereas boreal forests consist of primarily large tracts of forest dominated by a few species. Perhaps these structural differences between the boreal and temperate forest are primarily relevant to medium-sized birds.

Future Research

All of the above results are consistent with the hypothesis that avian body-size clumps reflect the hierarchical structure of biomes. These results provide more confirmation to the textural-discontinuity hypothesis, but more examples are needed. Future studies should compare the body-size distributions of avifauna from other areas in the temperate and boreal biome. For example, boreal and temperate avifauna lists from the eastern Palearctic biogeographic realm could be compared. In this comparison, do the same body-size clumps appear as what was revealed in this study? What about comparisons between avifauna in fragmented and unfragmented landscapes; do the medium-sized species tend to be the most affected in fragmented landscapes? Additional research in this area will be fruitful to determine the generality of clumps.

Summary and Conclusions

The match between the body-size clump structure of eastern North American and European boreal and temperate avian body-size clumps suggests that the hierarchical landscape structure of each biome is similar between the two continents. Comparing the number of species in each clump, fewer European than eastern North American bird species were present in the small and medium size ranges, but more European than eastern North American bird species were present in the large size range. I hypothesized that the cross-continental difference in the number of species at the different size ranges was a result of historical landscape changes in each continent. The highly fragmented European landscape contained less resources for small- and medium-sized birds, but more resources for large birds. The larger number of body-size clumps found in eastern North American avifauna lists (both biomes) was also attributed to the higher degree of landscape fragmentation in Europe than in eastern North America. Further, comparisons within a continent revealed that the avian body-size clump structures of the boreal and temperate zones matched at the small and large size ranges, but some mismatch occurred at the medium size range. This was interpreted as an indication that landscape structure between the two biomes are similar at small and large scales, but different at middle scales. Overall, these results provide more evidence that animal body-size clumps may reflect the hierarchical structure in landscapes.

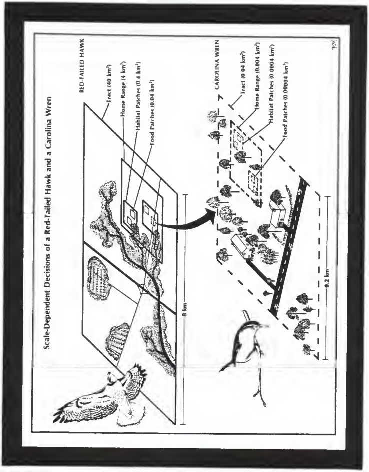
CHAPTER 4

RESPONSES OF BIRDS TO SCALE-DEPENDENT LANDSCAPE STRUCTURE

Introduction

The range of scales at which organisms respond to landscape structure is defined by the *spatial extent*, or largest area that is sampled by each organism, and the *spatial grain*, or minimum size of objects sampled by each organism (Kotliar and Wiens 1990, Wiens 1990). Although extent and grain are the upper and lower boundaries of scale relevant to an animal, there is a hierarchy of decisions made by all animals within this range of scales (Kotliar and Wiens 1990, Holling 1992). Imagine a wren and a hawk flying over a landscape in search of a habitat that provides foraging sites, nesting sites, and adequate protection from predators. Both birds go through a nested set of hierarchical decisions, but each bird responds to different landscape attributes as a function of its body size. Using estimated home range areas (Schoener 1968) as a reference, the small wren samples small areas and selects small objects, whereas the large hawk samples large areas and large objects (Figure 4-1). That is, birds of different size classes pay attention to differently scaled attributes in an environment. The range of scales pertinent to a bird is defined by both grain and extent (Wiens 1990, Turner and Gardner 1991, Kotliar and Wiens 1990). However, how large of an area are different species responding to landscape structure and

Figure 4-1. Different scale-dependent landscape structures perceived by a wren and a hawk. Notice that the only overlap in the types of objects sampled by the two birds is at the food patch level for the hawk and at the tract level for the wren. At the upper boundary of scales relevant to a wren, the wren searches a region (spatial extent of 0.1 - 0.4 km2) to locate a tract of land (spatial area of 0.01 - 0.04 km^2) that has ample resources to survive harsh times; next, the wren searches this tract to establish a home range (spatial area of 1000.0 - 4000.0 m^2); at the next scale, the wren searches its home range for suitable foraging patches (spatial area of 100.0 - 400.0 m^2); then, within these foraging patches the wren locates areas (spatial area of 10.0 - 40.0 m^2) where food is abundant; and at the smallest scale, the wren searches these areas where food is abundant for its prey (spatial grain of 0.1 - 1 cm^2). The hawk has a similar nested set of hierarchical decisions, but it selects much larger areas and objects at each comparable scale (e.g., home range equals a spatial area of 2.0 - 4.0 km^2).



Scale-Dependent Decisions of a Red-Tailed Hawk and a Carolina Wren

RED-TAILED HAWK
Tract (40 km^2)
Home Range (4 km^2)
Habitat Patches (0.4 km^2)
Food Patches (0.04 km^2)
8 km
CAROLINA WREN
Tract (0.04 km^2)
Home Range (0.004 km^2)
Habitat Patches (0.0004 km^2)
Food Patches (0.00004 km^2)
0.2 km
RM

what actual sizes of objects (e.g., tree patches) do birds respond to within this area?

Many ecologists have recognized that the range of scales relevant to animals is an important determinant in the spatial distribution and population dynamics of animal populations (Levin 1992, Wiens et al. 1993, Wiens 1989). Both landscape ecologists and behavioral ecologists have identified habitat selection and movement by animals as being important to theories and ecological models developed in both fields (Wiens et al. 1993, Turner et al. 1989, Hansson 1991, Pulliam et al. 1992, Turchin 1991, Levin 1992, Krebs and Davies 1991, Bell 1991, and Mangel and Clark 1988). However, traditional behavioral ecologists conduct research at small spatial scales whereas landscape ecologists operate at large scales. Behavioral ecologists have conducted empirical studies on habitat selection and movement by animals within their home range (e.g., Gass and Montgomerie 1981). However, empirical studies on how different animals respond to landscape-level structure (e.g., above the level of the home range) are virtually nonexistent (Lima and Zollner 1996; although see With 1994). Generally, ecologists in both fields recognize the importance of processes and phenomena that operate at both small and large scales, but research programs in landscape and behavioral ecology have little common ground. Thus, a need exists for the fusion of behavioral ecology with landscape ecology; essentially, a "behavioral ecology of ecological landscapes" should be developed (Lima and Zollner 1996).

There are some theoretical foundations for exploring the effects of large-scale landscape structure on animal population and movement. Island biogeography theory (MacArthur and Wilson 1967) and the subsequent development of metapopulation theory (Gilpin and Hanski 1991) address the potential effects of landscapes on local and regional animal population dynamics. When animals are dispersing from one habitat patch to another, how animals respond to the landscape matrix that exists between habitats is vital to the ability of certain animals to disperse (Harris 1984, Fahrig and Paloheimo 1988, Opdam 1990, Hanski 1991). This dispersal ability may be important to the viability of species in a region (Gilpin and Hanski 1991, Burkey 1989, Stacey and Taper 1992). The landscape matrix may or may not be suitable for dispersal, depending on how patterns in a landscape (at different scales) affect an organism.

The pattern of landscape structure changes as one goes from small to large scales (Turner 1989, Gardner et al. 1987, Powell 1989, Levin 1992). What may be a fairly homogeneous landscape at one scale may be quite heterogeneous at another scale (see Kotliar and Wiens 1990). As Wiens (1989) puts it, ". . . virtually all community patterns and processes are likely to exhibit some degree of scale-dependency." Recently, ecological models have incorporated patchiness of a landscape at different scales to see how this affects animal movement and the growth and persistence of populations (e.g., Gardner et al. 1993). These models have been quite informative, illustrating the potential effects of scale-dependent landscape pattern on population dynamics and movement of animals; however, assumptions about animal movement and perception in these models, especially at the level of the landscape, were not based on empirical studies. In the natural world, the scale-dependent effects of landscape structure depend on how different animals perceive their environment. Attempts to determine the scales at which species respond to structure have been limited so far (Wiens 1995, Opdam 1991, Harrison 1992).

At the level of the landscape, two questions have plagued ecological modellers, landscape ecologists, and conservationists alike: 1) at what scales do different species perceive critical landscape structure and, 2) in terms of the sizes and the quantities of objects at each scale, what is the spatial arrangement necessary to attract certain species? Because many ecological and behavioral traits are correlated with body size (Brown 1995), perhaps size may be a useful way to gain insight about how birds select landscape structures at a variety of scales. However, when using the variance of one variable, such as body mass, to predict the variance of another variable (e.g., the scales at which birds respond to landscape structure) one must use caution in the causal interpretation. Other factors may play a significant role. For example, McNab (1963) demonstrated that basal metabolic rate was linearly proportional to home range area, but Harestad and Bunnell (1979) showed that trophic status and habitat productivity also has a large influence on the home range area of an animal. Nevertheless, Wiens (1989) hypothesized that body mass may be an appropriate variable to predict the relevant scales of many organisms of different sizes.

In one such analysis, Holling (1992) hypothesized that bird masses would be grouped into several distinct "clumps" that reflect different structures in a landscape from small to large scales. Clumps are essentially groups of similar-sized animals that are separated by a significant gap in the masses from one group to the next (see chapter 2). Birds in each body size clump are theoretically responding to the same sizes of structural objects in a landscape within the same range of scales because the size of an animal constrains the sizes of objects available to it (Holling 1992). Animal body-size clumps might be used as a powerful technique to address the range of scales relevant to different sizes of birds. What is needed is a way to test whether birds in each body-size clump respond to different-sized geometric features within a landscape.

Suburban landscapes are good systems to explore questions about the scales relevant to birds because the spatial geometry of canopy coverage in these landscapes changes in a variety of ways from small to large scales. Suburban landscapes have been drastically transformed at potentially all scales, and a fraction of the native North American birds seem to flourish in suburban environments (Geis 1974; Emlen 1974; and Guth 1980). Recent avian studies in suburban environments stress that habitat structure is the primary factor that determines bird diversity (Penland 1984; Horak 1986; Sexton 1987; Baines 1988; and Stenberg 1988). But at what scale? One way to determine the scales at which different bird species respond to structure is to compare the types of birds that use these fragmented suburban landscapes.

The scale of the investigation depends upon the organism and the question (Wiens 1993); many different levels in the decision hierarchy could be studied (refer to Figure 1). A researcher could ask a question about what types of habitat patches a bird forages in within its home range; this researcher would focus on the spatial arrangement of objects below the home range scale of the bird in question. Or, one could ask what types of food patches does a bird forage in within its habitat, focusing on the spatial arrangement of objects below the habitat patch level. Also, it is important to recognize that the range of scales relevant to an organism may be dependent on the life history stage of that organism (Levin 1992). During the breeding season, birds look for a potential home range area in which to nest whereas during the spring, migrating birds look for stopover sites (Moore and Simons 1992) and short-distance dispersers look for specific habitats when moving from one area to another (i.e., dispersing sites). The scale-dependent structure that attracts a bird to an area may be significantly different for these two seasons.

The focus of my study was on the landscape structure relevant to birds when choosing a home range during the breeding season and when choosing a stopover site or dispersing site during the spring migration season. Thus, the decision hierarchy level of birds that was addressed in this study was at the landscape-level. I limited the scope of the study only to birds that forage or nest in the tree canopy and to the question of how they responded to patches of canopy cover (at different scales) in different landscapes. The objectives of this study were (1) to ascertain whether body-size clumps could be used to determine the scale(s) at which different sizes of birds make landscape-level decisions during the spring and summer, (2) to develop hypotheses about how large an area is used by birds when responding to landscape structure, and (3) to develop hypotheses about the patch sizes within these areas sampled by different sizes of birds.

Methods

Overview

The purpose of this study was (1) to determine whether body-size clumps could be used to estimate the scale(s) at which different sizes of birds make landscape-level decisions during the spring and summer, (2) to develop hypotheses about how large an area is used by birds to respond to structure when they choose home ranges, stopover sites, and dispersing sites, and (3) to estimate the sizes of objects sampled by birds within these areas. To do this, I conducted my analyses in five steps, and the following is an overview of these five steps (specifics are given later). First, I obtained lists of bird counts (#birds observed/hour) from reported surveys conducted in various suburban landscapes across North America. I selected as many different suburban sites (with reported surveys) as possible to assure a wide range of landscape patterns. Also, these suburban sites were situated in different regions of North America in order to represent different ecosystems and bird species. The rationale behind this is that if body-size were a good predictor of the spatial scales relevant to a species, then it should not matter which ecosystem and species are included in the study. I separated the bird surveys into two groups: (1) surveys that were conducted during the breeding season, and (2) surveys that were conducted during the spring migration season. This was done because birds may be responding to landscape structure at different scales during these seasons. Only birds that forage or nest in the tree canopy were used in the analyses. All species in the censuses were standardized to the number of birds sighted per hour.

Second, I wanted to group these suburban species into size categories that theoretically represent a suite of species that respond to landscape structure within the same range of scales. The purpose of this was to see whether body-size clumps could be used to evaluate the scales at which different sizes of birds respond to landscape structure. Because all of the suburban sites used in this study were in the temperate forest biome, I used the body-size clumps detected for the temperate forest biome in chapters 2 and 3. However, of the 10 clumps detected for the temperate forest biome, only the first 8 clumps were used because large birds were not used in the subsequent analyses. For each suburban site, I summed the reported bird counts (from step 1) for each of the 8 body-size clumps. Ultimately, counts in each body-size clump were used in correlation analyses (see step 4) to determine whether body-size clumps could be used to develop hypotheses about the relevant spatial scales of birds during the spring and summer.

The third step was to gather aerial photographs of four different spatial areas (0.2 km^2, 1.5 km^2, 25.0 km^2, and 85.0 km^2) that were positioned over the exact location of each suburban bird survey site. At each spatial area, I measured the percent tree canopy cover of different patch sizes ranging from small to large canopy patches (11 categories in all). Essentially, each patch size category represented a limited range of canopy patch sizes.

The fourth step was to run multiple regression analyses at each spatial area to determine if the variation of percent tree cover for the 11 patch size categories could predict the variation in bird counts in each body-size clump (across all sites). These analyses essentially determined which area size and patch size best predicted the variation in bird counts. Throughout the paper, "best prediction area" (BPA) is used to describe the size of an area (containing tree canopy patches) that best predicted the variation in the bird counts. Likewise, "best patch size" (BPS) refers to a category of patch sizes that best predicted the variation in the bird counts. Significant correlations found in this step were hypothesized to reflect the area and patch sizes responded to by birds when sampling landscape structure.

Suburban Bird Data Sets

Criteria for selection of a suburban site was that the report contained a comprehensive suburban bird list, including information to calculate the number of birds observed/hour for each species, spring and/or summer surveys, an adequate explanation of how birds were surveyed, and the exact locations of the survey routes. All surveys used a line-transect method (Emlen 1974) to estimate bird abundance and diversity; researchers walked down a road and counted the number of birds seen or heard within approximately 45 meters on either side of the transect. The landbird faunal lists from each suburban site were compiled from several different studies. Several sites within each study were normally surveyed by a researcher; thus, bird counts specific to several independent sites could be derived from one study. The number of sites in each city were as follows: Amherst, MA had three separate sites and Springfield, MA had one site (DeGraaf and Wentworth 1981); Austin, TX had three sites (Sexton 1987); Blacksburg, VA had seven sites (Lucid 1974); Chicago, IL had eight sites (Guth 1980); Seattle, WA had six sites (Penland 1984); and Vancouver B.C. had seven sites from Lancaster (1976) and four sites from Weber (1972). Only diurnal landbird species were included in my analyses; all reported exotics, nocturnal species, high aerial screeners, and waterbirds were excluded because most studies did not survey these birds. The cities are located in eight different ecoregions: Amherst & Springfield - Northeastern Highlands; Austin - Texas Blackland Prairies and Central Texas Plateau; Blacksburg - Central Appalachian Ridges and Valleys; Chicago - Central Corn Belt Plains; and Seattle/Vancouver - Puget Lowland (Omernik 1987).

Reported censuses were separated into two groups: (1) birds sighted only during the breeding season, and (2) birds sighted during the spring migration. The breeding season was defined as the period of time during the summer in which most of the spring migrants have stopped migrating through an area and the bulk of the fall migrants have not started to fly south (the exact dates depend on what part of the country the city was located). These dates were either gathered directly from the reports or a local expert was contacted. A total of 31 sites from Chicago, Amherst, Springfield, Austin, Blacksburg, and Vancouver (both Lancaster's and Weber's study) was used to provide data for the breeding season (Appendix D).

The spring migration period was defined as the period of time in which migrating birds began to arrive in an area and when the numbers of birds flying through an area began to taper off (again the exact dates depend on where the city was located). Again, determination of these dates was based on consultation with local experts or from dates listed in the reports. A total of 23 sites from Chicago, Seattle, and Vancouver (both Lancaster's and Weber's study) was used for the spring migration (Appendix D).

Only birds that forage and/or nest in the tree canopy were used because only tree canopy coverage was quantified from aerial photographs. Birds that either nest and forage on the ground/low shrub layer or exclusively nest on the ground (even though they could forage in the trees) were excluded from the breeding season analyses. Birds that foraged exclusively on the ground were deleted from the spring migration season analyses. The Birder's Handbook (Ehrlich et al. 1988) was used to derive such natural history strategies. Also, it was questionable whether several species primarily used tree canopy because they have been classified as "adapted" to conditions in suburban areas. These birds may be primarily using other factors besides canopy cover to evaluate the suitability of an area. For example, cardinals (*Cardinalis cardinalis*) are known to use bird feeders in suburban areas, and they may be responding to the availability of feeders not the amount of canopy cover. If a species were listed as breeding in suburbs in The Birder's Handbook (Erhlich et al. 1988), they were classified as "urban adapted." Also, a 5-year urban bird study in Amherst, MA (Goldstein et al. 1986) was consulted, and those birds that were listed as relatively insensitive to vegetation volume were classified as "urban adapted." Such birds were excluded from the spring and summer data lists.

In order to compare bird counts across different sites, I first standardized bird counts of each species by calculating the mean number of birds sighted per hour per site. Typically, a mean number of observed birds per site was reported. I took this mean number and divided it by the time it took to census the site, and this number was standardized to the number of birds observed per hour. Although small biases could result from more transects being done in one survey versus another (i.e., more area covered), this source of bias was considered negligible because all authors picked sites within fairly homogeneous areas at large scales. However, for species that were recorded in several cities, state to state differences in the abundance of a specific species could bias the analyses. For these species, BBS counts from each state (Chandler 1986) were compared to see if an overall difference in abundance existed between states. From BBS counts, if a species were at least 1.5 times more abundant in one city versus another, then density was standardized for this species across these cities. For example, if a species were recorded in Vancouver and Amherst but it was 8 times more abundant in Vancouver (according to BBS counts), then potentially the counts recorded in Vancouver were inflated due to more birds occurring in the Vancouver area. In this example, the standardized bird count (calculated as above) of that one species in Vancouver would be divided by 8. For spring migrants that used a suburban location as a stop-over site but did not breed in the area, BBS surveys conducted north of the actual cities (where these migrants breed) were compared to determine if an overall difference in abundance existed between states.

Body-size Clumps

Eight of the ten body-size clumps determined from the clump analysis of temperate forest avifauna lists (chapters 2 and 3) were used in the subsequent analyses (0.0 - 6.9 grams; 7.0 - 16.5 grams; 16.6 - 21.6 grams; 21.61 - 33.75 grams; 33.76 - 61.60 grams; 61.7 - 184.0 grams; and 185.0 - 576.5 grams). The procedure for detecting these clumps was outlined in Chapter 2. Only 8 of the 10 body-size clumps detected in chapter 2 were used because the largest bird in the suburban faunal lists weighed less than 576.5 grams. For ease of reporting the results, the 8 size categories were assigned numbers in ascending order starting with 1 for the smallest size category (0.0 - 6.9 grams) to 8 for the largest size category (185.0 - 576.5 grams). The number of birds observed/hr for all species within a clump were then summed for each of the 8 body-size clumps. For each clump, the total number of birds observed/hr was the dependent variable in the multiple regression described below.

Measurement of Canopy Patches from Aerial Photographs

In 1994, I visited each of the suburban sites to determine the exact locations of the surveys and to contact local property appraisal offices and state agencies in order to obtain aerial photos. It should be noted that ecologists typically refer to scale in terms of spatial extents and grain whereas cartographers and geographers typically refer to the scale in terms of ratios (e.g., 1:24,000). To avoid confusion about what I mean when I say "scale", I will refer to the geographer's use of the word scale as "nominal scale". I obtained aerial photos at three different nominal scales (1:2400, 1:24,000, and 1:40,000) in order to measure landscape structure from small to large areas. At the first nominal scale of 1:2400, aerial black & white photos were obtained from either local property appraisal offices of the respective city or the State Department of Transportation; all photos were centered over each survey site and the paper size of the photo was at least 20 in. X 20 in. At the second nominal scale of 1:24,000, aerial black & white photos were obtained from the Department of Transportation in each state or when not available, from the U.S. Department of Agriculture: Agriculture Stabilization and Conservation Service (USDA-ASCS, Aerial Photography Field Office, 2222 West 2300 South, P.O. Box 30010, Salt Lake City, UT 84130-0010). These photos were also centered (approximately) over each survey site and the paper size was at least 9 in. X 9 in. At the third nominal scale of 1:40,000, aerial photos were obtained from the National High Aerial Photography (NHAP) of the U.S. Department of the Interior. Photos at this scale were ordered through the U.S. Geological Survey Department (USGS, Stennis Space Center, Earth Science Info Center, Building 3101, Stennis Space Center, MS 39539), and produced at the U.S. Geological Survey EROS Data Center (EROS Data Center, Sioux Falls, SD 57198). For sites in Vancouver, photos were obtained from Maps Division of British Columbia (MAPS - B.C., Ministry of Crown Lands, Surveys and Resource Mapping Branch, Parliament Buildings, Victoria, British Columbia, Canada, V8V 1X5).

Again, photos were centered (approximately) over each survey site and the paper size was at least 9 in. X 9 in.

All aerial photos used in the analyses were taken approximately within the same year as when the bird surveys were done (+/- 3 years). Photos were taken during the spring/summer (i.e., leaves were on the trees) and the location of the survey sites was verified with prominent landscape features in the photo (i.e., roads).

Spatial area of measured tree canopy. Aerial photographs of four different spatial areas were used in subsequent analyses. At the smallest nominal scale (1:2400), two different rectangular areas were used in the analyses. The smallest spatial area was 0.2 km^2 and this size was large enough to encompass the home range of all the birds in this study (Schoener 1968). The other spatial area was 1.5 km^2 and it covered the surveyed area and area surrounding the location of the suburban censuses. At the next nominal scale (1:24,000), the rectangular area was 25.0 km^2 and was centered over a suburban site. At the largest nominal scale (1:40,000), the rectangular area was positioned over a suburban site (usually several sites were covered in each city) and encompassed 85.0 km^2. Thus, for each site, a total of four spatial areas were used in all analyses.

The pixel size (or resolution) for each nominal scale was standardized across all sites; this was necessary because in some cases, the nominal scale of the aerial photograph did not exactly equal 1:2400, 1:24,000, or 1:40,000. At 1:2400, the pixel size was

36.0 m^2, at 1:24,000 the pixel size was 119.0 m^2, and at 1:40,000 the pixel size was 330.6 m^2.

For all aerial photos, tree canopy cover was traced onto a clear acetate film, scanned into a computer (250 dots per inch), and transferred into a drawing program (Ultra Paint*). Tree canopy cover was colored black and the open areas were red; this was done so that the amount of land and the percent cover could be calculated in the GIS program Map II*. All images used in the analyses were standardized to the above listed spatial areas. Once an image was in Map II, a clumping command was used to measure the size of each tree canopy patch. These measurements were then transferred into a spread sheet (Microsoft Excel*) to calculate the percent cover of the 11 different canopy patch categories (see below).

Canopy patch categories. Tree canopy patches measured in Map II were grouped into 11 canopy patch categories; essentially, each canopy patch category represented a limited range of patch sizes. These patch categories were used to determine, statistically, best patch size of birds in each body-size clump and to better represent the composition of a site (i.e., was the percent canopy cover at a site represented primarily by large or small patches?). The percent canopy cover of each of the 11 patch categories was calculated in two steps. The steps below refer to one spatial area of a site but they are applicable to all four spatial areas of each site.

Step 1. Each of the 11 canopy patch categories were defined by their smallest patch size; this patch size was a filter that excluded all other patches of smaller sizes (Table 4-1). For ease of reporting the results, the 11 canopy patch categories were assigned letters in

Table 4-1. Tree canopy patch categories for each of the four spatial areas (0.2 km^2 and 1.5 km^2, 25.0 km^2, and 85.0 km^2). The smallest canopy patch size that was included in each category is listed. At 0.2 km^2 and 1.5 km^2, the jump from one category to the next was 360.0 m^2; at 25.0 km^2, the jump from one category to the next was 23800.0 m^2; at 85.0 km^2, the jump from one category to the next was 132240.0 m^2.

SPATIAL AREA	TREE CANOPY PATCH CATEGORIES (m^2)										
	A	B	C	D	E	F	G	H	I	J	K
0.2 km^2	36.0	396.0	756.0	1116.0	1476.0	1836.0	2196.0	2556.0	2916.0	3276.0	3636.0
1.5 km^2	36.0	396.0	756.0	1116.0	1476.0	1836.0	2196.0	2556.0	2916.0	3276.0	3636.0
25.0 km^2	2.4990 X 10^3	2.6299 X 10^4	5.0099 X10^4	7.3899 X 10^4	9.7699 X 10^4	1.2150 X 10^5	1.4530 X 10^5	1.6910 X 10^5	1.9289 X 10^5	2.1670 X 10^5	2.405 X 10^5
85.0 km^2	6.9420 X 10^3	2.0530 X 10^5	4.0366 X 10^5	6.0202 X 10^5	8.0038 X 10^5	9.9874 X 10^5	1.1949 X 10^6	1.3955 X 10^6	1.5938 X 10^6	1.7922 X 10^6	1.9244 X 10^6

ascending order starting from patch category A with the smallest filter to patch category K with the largest filter. For example, patch category A had the smallest filter and all patches recorded in an image were included in this category. The next patch category (B) had a larger filter and excluded patches that were smaller than the size of this filter. This procedure continued until the largest patch category (K) contained only the largest canopy patches in an image.

Step 2. The percent canopy cover represented by a patch size category was calculated by taking the total area occupied by canopy and dividing by the total area at a particular spatial area. In essence, as the size of the filter increased with each patch category, percent cover decreased because fewer canopy patches were recorded in the larger patch size categories.

Exploring the Spatial Areas and Patch Sizes of Birds in Different Size Categories

Overview. The purpose of this section is to determine the best prediction area (BPA) and best patch size (BPS) where the variation in the amount of canopy cover correlated with bird count variation (spring and summer). Significant correlations were interpreted as the scale(s) at which birds responded to canopy cover. Analyses were conducted in five steps. The outline below will refer to one bird-size category but is applicable to all 8 bird-size categories.

Step 1: deriving independent axes. Because the 11 patch size categories were highly correlated within each spatial area (i.e., a large patch of tree canopy also contains lots of smaller patches), a principal component analysis (based on a correlation matrix) was used to derive two independent axes for each of the four spatial areas.

Step 2: multiple regression. The purpose of this step was to determine at which spatial areas (if any) bird counts were correlated to the amount of canopy cover. The values along the two PCA axes (from step 1) were used in the multiple regression analyses as the independent variables for each spatial area; total number of birds counted/hour in a body-size category was the dependent variable. Thus, for a body-size category, four separate multiple regression analyses were run: one for 0.2 km^2, one for 1.5 km^2, one for 25.0 km^2, and one for 85.0 km^2. The squared correlation coefficients were used to evaluate which spatial area(s) best predicted the variation in bird counts. A squared correlation coefficient (r^2) was considered to be significantly high enough to suggest that birds were responding to canopy cover if it had a value greater than 0.5 and a P-value less than 0.05. If the correlation coefficient value was less than 0.5 but greater than 0.2 (and a P-value less than 0.05), the r^2 was considered significant only if the value was within 0.1 of the highest r^2 value calculated among the other three spatial areas. This was done because I was trying to determine, relatively, which of the four spatial areas gave the highest r^2 value.

Step 3: primary response to PCA I or II. This step was done to determine which of the two PCA axes explained most of the variation in bird counts. For spatial areas that had significantly high correlation coefficients (step 2), standardized partial regression coefficients were calculated to determine whether the PCA I or PCA II axis was significantly correlated to variations in bird counts. A standardized partial regression coefficient was considered to be significant if it had a P-value less than 0.05. In addition, a uniqueness index (SAS Institute 1994) was calculated to evaluate the relative importance of each axis. The uniqueness index determines whether a given predictor accounts for a significant amount of the variance of the dependent variable. The uniqueness index for a given PCA axis was considered to be significant if it had a P-value less than 0.05.

Step 4: best prediction area (BPA). If several spatial areas had significantly high r^2 values for a bird-size category (step 2), then I did an additional multiple regression. The purpose was to determine at which spatial area bird counts primarily were correlated to the amount of canopy cover. It was hypothesized that larger birds would respond to structure at larger spatial areas. In these multiple regressions, the PCA components that were entered were those significantly high partial regression coefficients determined in step 3. The resultant partial regression coefficients were compared and the spatial area with the highest partial regression coefficient was considered the best prediction area. Again, a uniqueness index (SAS Institute 1994) was calculated for each PCA axis.

Step 5: exploring best patch size (BPS). After determining the best prediction area for a bird size category (step 4), I then explored the best patch sizes that birds could sample in a landscape. In other words, which of the 11 patch size categories explained the variation in bird counts the best? It was hypothesized that smaller birds would respond to smaller patch sizes than larger birds. To determine the BPS, I ran simple regressions between bird counts of a size category and percent tree canopy cover at each of the 11 patch size categories for each best prediction area (BPA). Thus, 11 simple regressions were conducted at the BPA determined from step 4. I started with the r^2 of the smallest patch size and compared it to the r^2 of the next patch size; this comparison continued on up to the largest patch category. A patch size category that gave the highest correlation coefficient (above 0.3) with a sharp drop in the correlation coefficient just before this "peak" was considered as the BPS of birds in a size category. If a bird-size category had a sharp drop in the correlation coefficient just after a peak r^2, then the range of patch size categories before this sharp drop was considered as the best patch sizes of birds in a size category. If no peak r^2 could be determined, BPS was not estimated.

Results

Bird Counts for Suburban Sites

Spring surveys. Bird counts (# of birds/hr) were quite variable in each of the size categories from one site to the next (Table 4-2); totals ranged from the Lake Forest site that had the highest bird counts in most of the size categories (except in 1, 2, and 8) to the DT and FC sites in Lancaster's Vancouver study that had no birds recorded in most of the size categories (except for the 8 category of the DT site). Appendix E contains the bird counts for each species across all sites.

From BBS surveys, black-capped chickadee, rufous hummingbird, wilson's warbler, yellow warbler, yellow-rumped warbler, and downy woodpecker had different counts (1.5 times or greater). Suburban counts of these species were changed to standardize for overall differences in abundance reported in BBS surveys of each state (Appendix E).

Summer surveys. Bird counts (# of birds/hr) were quite variable in each of the size categories from one site to the next (Table 4-3); count totals ranged from MT and OP sites that had birds recorded in all categories to North Central Chicago (NCCH), Addison, DT, FC, WE, and McBryde Village sites that had 7 of the 8 bird-size categories with no birds recorded. Appendix F contains the bird count for each species across all sites.

From BBS surveys, black-capped chickadee, rufous hummingbird, and downy woodpecker had different counts (1.5 times or greater). Suburban counts of these species were changed to standardize for overall differences in abundance reported in BBS surveys of each state (Appendix F).

Percent Tree Canopy Cover of Each Patch Size Category

Percent tree canopy coverage at each patch size category for each of the suburban sites (both spring and summer) of the four spatial areas are listed in Appendix G and Appendix H. Percent cover could be quite variable from one spatial area to the next for each site; for example, Lake Forest in Chicago had the greatest amount of cover in the largest patch size category (K) at 0.2 km^2 and 1.5 km^2,

Table 4-2. Bird counts (#birds/hour) of different size categories from Spring bird censuses. All birds characterized as primarily tree canopy users*.

SITES	BIRD-SIZE CATEGORIES (grams)							
	0 - 6.9 (g)	7.0 - 16.5 (g)	16.6 - 21.6 (g)	21.61 - 33.75 (g)	33.76 - 61.6 (g)	61.7 - 115.0 (g)	115.1 - 184.0 (g)	185.0 - 576.5 (g)
Skok	0.6923	7.1538	1.6154	2.3077	0.9231	0.2308	0.0	0.0
SEVA	2.1250	2.1302	0.7500	2.5000	1.5000	0.1250	0.8750	0.0
Wllm	0.7407	7.7778	4.6296	2.5000	2.9630	0.9259	0.5556	0.0
NCCH	2.0000	1.5000	1.0000	3.0000	1.0000	0.5000	0.0	0.0
Lake For	1.2000	7.4000	5.4000	6.9000	3.8000	1.4000	1.6000	0.0
Addis	0.0	2.7500	1.2500	0.1250	0.5000	0.0	0.0	0.0
Ballard	4.5924	0.9099	0.0	0.1846	0.0	0.0	0.0	4.0616
Central	5.8232	7.0683	0.4154	0.9231	0.7846	0.0	0.0	8.6310
Madronna	3.8078	3.7353	0.0000	0.1385	0.0	0.0	0.0	6.9233
Ravenna	3.2693	3.4682	0.3692	0.2769	0.0	0.0	0.0	5.1694
NorthEnd	4.4309	11.5849	0.6462	0.2308	1.2923	0.4616	0.1385	12.1849
Queen Anne	1.7462	1.0616	0.1385	1.6616	0.3692	0.0	0.0	2.5847
Churchill	4.3100	11.7300	2.7000	2.1000	0.0600	0.8400	0.0600	8.4000
Ferguson	0.3058	1.0495	0.5138	0.2055	0.0	0.0	0.0	0.9248
Spruce	0.3678	0.6098	0.0	0.0	0.0	0.0813	0.0	0.2439
Yukon	1.6172	2.1625	0.0	0.3922	0.0	0.2353	0.0	0.1569
CW	2.1562	2.0554	0.0	0.3849	0.0	0.0	0.0	0.2490
MK	0.0226	0.1391	0.0	0.0	0.0	0.0	0.1359	0.1359
FC	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
QE	0.1094	1.2905	0.0	0.0	0.0	0.0	0.0	0.3170
SH	2.2220	2.1557	0.1585	0.4981	0.0	0.4981	0.0	2.9885
WE	0.0302	0.1811	0.0	0.0	0.0	0.0	0.0	0.0
DT	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5660

Table 4-2 (cont.)

* excluding exotics, urban adapted birds (cardinal, blue jay, common grackle, mourning dove, chipping sparrow, mockingbird, house finch, cowbird, house wren, great-tailed grackle), and a few birds that were sighted in the surveys but left out because they foraged primarily on the ground (rufous-sided towhee, purple finch).

Table 4-3. Bird counts (#birds/hour) of different size categories from Summer bird censuses. All birds characterized as primarily tree canopy users*.

SITES	**BIRD-SIZE CATEGORIES (grams)**							
	0 - 6.9 (g)	7.0 - 16.5 (g)	16.6 - 21.6 (g)	21.61 - 33.75 (g)	33.76 - 61.6 (g)	61.7 - 115.0 (g)	115.1 - 184.0 (g)	185.0 - 576.5 (g)
MT	0.1000	2.0000	1.0000	0.7000	5.4500	0.8000	0.1500	0.5500
OP	0.0500	2.9500	6.8000	5.9000	5.3500	0.7500	1.0000	0.3500
YT	0.0	0.0750	2.5000	0.2500	1.3500	0.0	0.0500	0.0
FP	0.0	1.5980	0.0	1.0670	1.9540	1.2420	0.0	0.0
HP	0.0	1.0220	0.0	1.3580	2.7160	6.1450	0.0	0.0
T	0.0	3.5000	4.0210	1.0390	3.5010	5.3190	0.0	0.0
SPRING	0.0500	0.1500	0.1500	0.5500	0.0500	0.0	0.0	0.1500
HIGH	0.0	0.2380	0.9520	2.3810	1.6660	0.2380	0.0	0.0
AIRPORT	0.0	1.9040	0.0	0.2380	0.0	0.0	0.0	0.0
DRAPER	0.0	2.1430	0.2380	0.2380	0.7140	1.6670	0.2380	0.0
TERRACE	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
MCBRYDE	0.0	0.2380	0.0	0.0	0.0	0.0	0.0	0.0
OAK	0.0	2.3810	1.9050	4.9207	0.0	0.2380	0.4760	0.0
BLACKWO	0.0	3.0950	0.2380	4.6033	5.4770	2.8570	1.6670	0.0
LAKE FOR	0.1440	13.4020	1.7310	4.9030	2.8840	0.8660	1.7310	0.0
ADD	0.0	0.9380	0.0	0.0	0.0	0.0	0.0	0.0
NCCH	0.0	0.0	0.0	0.1000	0.0	0.0	0.0	0.0
NEVA	0.0	3.5960	1.8750	1.2510	0.6250	0.3130	0.6250	0.0
SEVA	0.0	0.7280	0.0	0.0	0.0	0.0	0.2080	0.0
SKOK	0.0	0.5210	0.3910	0.3910	0.5220	0.1300	0.0	0.0
WILM	0.0	2.0045	0.7220	5.0540	0.7210	1.6030	0.3210	0.0
WINN	0.0	6.1500	1.8000	6.3000	3.6000	0.6000	1.5000	0.0
CW	0.0	4.7010	0.0	0.2710	0.0	0.0	0.0	0.2710

Table 4-3 (cont.)

	0 - 6.9 (g)	7.0 - 16.5 (g)	16.6 - 21.6 (g)	21.61 - 33.75 (g)	33.76 - 61.6 (g)	61.7 - 115.0 (g)	115.1 - 184.0 (g)	185.0 - 576.5 (g)
MK	0.0450	1.5820	0.0	0.0	0.0	0.0	0.0	0.4970
DT	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5650
FC	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4070
Œ	0.0	1.2650	0.0	0.0900	0.0	0.0	0.0	0.2940
SH	0.0	10.0340	0.0	0.0450	0.0	0.0	0.0900	2.1240
WE	0.0	1.3560	0.0	0.0	0.0	0.0	0.0	0.0
CHURCH	0.3280	14.6200	0.0	0.6020	0.1090	0.0	0.0	1.6360
FERGUS	0.0	2.1580	0.0	0.1030	0.1030	0.0	0.0	0.0000
SPRUCE	0.0	1.0410	0.0	0.0	0.0	0.0	0.0	0.7440
YUKON	0.0	2.5030	0.0	0.2570	0.0	0.0	0.0	0.0

* excluding exotics, urban adapted birds (cardinal,blue jay, common grackle, mourning dove, chipping sparrow, mockingbird, house finch, cowbird, house wren, Great-tailed grackle), and a few birds that were sighted in the surveys but left out because they nest on the ground (MacGillivray's warbler, Wilson's warbler, mourning warbler).

but not at 25.0 km^2 and 85.0 km^2 where Lake Forest had lower percent cover in the largest patch size category (K).

Spring Surveys: Principle Component Analyses (PCA) and Multiple Regression Analyses

All sites were used in the PCA and subsequent multiple regression analyses for 7 of the 8 bird-size categories; category 8 was analyzed with all of the sites except the Chicago sites. The Chicago sites were left out because it was believed that the researcher in the Chicago area did not census the American crow (the main bird in bird-size category 8).

PCA results. Across all scales and sites, the first two PCA components explained greater than 97% of the variance in the percent cover of the 11 canopy patch categories. The first PCA component (PCA I) was interpreted as the percent cover axis and reflected a gradient of sites ranging from those with little percent cover by primarily small patches to sites with large percentages of cover by large patches (typically greater than 95% of the variation was explained by PCA I). When two sites had similar total percent cover, the site with a larger percentage of cover by larger patches was given a higher score. The second PCA component (PCA II) was interpreted as a fragmentation axis, sites with a higher small to large object ratio were separated from sites with a lower small to large object ratio (typically less than 5% of the variation was explained by PCA II).

Spring multiple regression results. For most bird-size categories in the spring, squared correlation coefficients (r^2) were relatively high at 1:2400 (0.2 km^2 and 1.5 km^2) and 1:40,000 (85.0 km^2) (values ranged from 0.35 to 0.69); exceptions were category 1 which had no significantly high r^2 values, category 2 and 6 which did not have a significantly high r^2 value at 85.0 km^2, and category 8 which had significantly high r^2 values at 1.5 km^2 and 25.0 km^2 (Table 4-4). All size categories had relatively small r^2 values at 25.0 km^2 except for the 8 category that had an $r^2 = 0.52$. Thus, during the spring migration season, bird counts in size categories 2 to 7 correlated with tree canopy cover at 0.2 km^2 and 1.5 km^2, counts in categories 3, 4, 5, and 7 correlated with canopy cover at 85.0 km^2, and counts in category 8 correlated with tree canopy cover at 1.5 km^2 and 25.0 km^2.

Standardized partial regression coefficients (Tables 4-5 & 4-6) indicated that at the spatial areas of 0.2 km^2 and 1.5 km^2, bird counts in the size categories from 2 to 7 were significantly correlated with percent canopy cover (PCA I: *P*-values and uniqueness indices < 0.05). More canopy cover equaled more birds within these areas. Conversely, standardized partial regression coefficients (Table 4-7) indicated that at the spatial area of 85 km^2, bird counts in size categories 3, 4, 5, and 7 were significantly correlated with the ratio of small to large canopy patches (PCA II: *P*-values and uniqueness indices < 0.05). A large ratio of small to large patches (i.e., more fragmentation) was correlated to more birds. For category 8, which had high r^2 values at 1.5 km^2 and 25.0 km^2, the bird counts were significantly correlated with percent canopy cover at 1.5 km^2 (more cover = more birds), but at 25.0 km^2, bird counts were significantly correlated with the ratio of small to large canopy patches (larger

Table 4-4. Squared correlation coefficients (r^2) for bird-size categories from multiple regression equations between Spring bird counts (#birds/hr) and percent tree canopy coverage at several different scales. Bold values indicate the highest r^2 among the four spatial areas.

SCALE (area)	BIRD-SIZE CATEGORIES (grams)							
	0.0 to 6.9 (g)	7.0 to 16.5 (g)	16.6 to 21.6 (g)	21.6 to 33.75 (g)	33.76 to 61.6 (g)	61.7 to 115.0 (g)	115.1 to 184.0 (g)	185.0 to 576.5 (g)
0.2 km^2	0.11	0.41*	0.50*	0.33	0.58*	0.49*	0.37	0.35
1.5 km^2	0.15	0.35*	0.55*	0.48*	0.69*	0.48*	0.60*	0.41*
25.0 km^2	0.12	0.23	0.23	0.28	0.30	0.22	0.30	0.52*
85.0 km^2	0.00	0.11	0.49*	0.53*	0.59*	0.36	0.59*	0.18

* P-value < 0.05 (df = 1)

Table 4-5. Standardized partial regression coefficients (*b*) for bird-size categories from multiple regression analyses of Spring bird counts (#birds/hr) and percent tree canopy coverage at 1:2400 (0.2 km^2).

Bird Size (grams)	***b* of PCA I**[1]	***b* of PCA II**[2]
0.0-6.9	0.2770	-0.1710
7.0-16.5	0.5750*	-0.2900
16.6-21.6	0.6880*	-0.1620
21.61-33.75	0.5640*	-0.0850
33.76-61.6	0.7610*	-0.0100
61.7-115.0	0.6410*	-0.2850
115.1-184.0	0.6070*	-0.0340
185.0-576.5	0.5390*	-0.2370

* P-value and uniqueness index < 0.05

1 Positive partial regression coefficients indicate that the counts of birds increase with an increase in percent tree canopy cover.
2 Positive partial regression coefficients indicate that the counts of birds increase with an increase in the ratio of large to small patches (i.e., less fragmentation).

Table 4-6. Standardized partial regression coefficients (*b*) for bird-size categories from multiple regression analyses of Spring bird counts (#birds/hr) and percent tree canopy coverage at 1:2400 (1.5 km^2).

Bird Size (grams)	***b* of PCA I**[1]	***b* of PCA II**[2]
0.0-6.9	0.2009	0.3390
7.0-16.5	0.5200*	0.2890
16.6-21.6	0.7390*	-0.0580
21.61-33.75	0.6830*	-0.1200
33.76-61.6	0.8290*	-0.0760
61.7-115.0	0.6950*	0.0320
115.1-184.0	0.7608*	-0.1520
185.0-576.5	0.6400*	-0.0690

* P-value and uniqueness index < 0.05

[1] Positive partial regression coefficients indicate that the counts of birds increase with an increase in percent tree canopy cover.

[2] Positive partial regression coefficients indicate that the counts of birds increase with an increase in the ratio of large to small patches (i.e., less fragmentation).

Table 4-7. Standardized partial regression coefficients (*b*) for bird-size categories from multiple regression analyses of Spring bird counts (#birds/hr) and percent tree canopy coverage at 1:40,000 (85.0 km^2).

Bird Size (grams)	*b* of PCA I[1]	*b* of PCA II[2]
0.0-6.9	-0.0270	-0.0410
7.0-16.5	-0.0240	-0.3370
16.6-21.6	0.1200	-0.6880*
21.61-33.75	0.1040	-0.7200*
33.76-61.6	0.1680	-0.7510*
61.7-115.0	0.1030	-0.5890*
115.1-184.0	0.3010	-0.7060*
185.0-576.5	-	-

* P-value and uniqueness index < 0.05

1 Positive partial regression coefficients indicate that the counts of birds increase with an increase in percent tree canopy cover.
2 Positive partial regression coefficients indicate that the counts of birds increase with an increase in the ratio of large to small patches (i.e., less fragmentation).

Table 4-8. Standardized partial regression coefficient (*b*) for the bird-size category of > 185.0 g from multiple regression analysis of Spring bird counts (#birds/hr) and percent tree canopy coverage at 1:24,000 (25.0 km^2).

Bird Size (grams)	*b* of PCA I[1]	*b* of PCA II[2]
185.0-576.5	0.1770	-0.7000*

* P-value and uniqueness index < 0.05

1 Positive partial regression coefficients indicate that the counts of birds increase with an increase in percent tree canopy cover.
2 Positive partial regression coefficients indicate that the counts of birds increase with an increase in the ratio of large to small patches (i.e., less fragmentation).

ratios of small to large objects = more birds) (Table 4-8: *P*-value and uniqueness indices < 0.05).

Spring best prediction area (BPA). Multiple regression of the three main PCA components at the nominal scale of 1:2400 (PCA I for 0.2 km^2 and 1.5 km^2) and 1:40,000 (PCA II at 85.0 km^2) revealed that bird-size category 2 had the highest standardized partial regression coefficient at 0.2 km^2 whereas the other bird-size categories from 3 to 7 had the highest standardized partial regression coefficients at 1.5 km^2 (Table 4-9). For birds of category 8, multiple regression of the three main PCA components at the nominal scale of 1:2400 (PCA I for 0.2 km^2 and 1.5 km^2) and 1:24,000 (PCA II for 25.0 km^2), the highest standardized partial regression coefficient was at 25.0 km^2 (Table 4-10). These results indicate bird counts in category 2 may primarily be correlated with percent cover of tree canopy at 0.2 km^2; birds in the categories from 3 to 7 may primarily be correlated with percent cover of tree canopy at 1.5 km^2, and birds in category 8 may primarily be correlated with the degree of fragmentation of tree canopy cover at 25.0 km^2. However, these results should be interpreted with caution because the P-values were not significant for the standardized partial regression coefficients or the uniqueness indices of most size categories (Table 4-9). Overall, the size of the best prediction area tended to increase with the size of the bird during the spring season.

Spring best patch size (BPS). At the BPA of 0.2 km^2, the plot of squared correlation coefficients for each patch size category are displayed for bird-size category 2 (Figure 4-2). From this plot, category 2 had a peak correlation coefficient at patch category A.

The other bird-size categories were not evaluated at 0.2 km^2 because this was not their best prediction area. For bird-size category 2, patch category A translated into an BPS of 36.0 - 360.0 m^2.

At the BPA of 1.5 km^2, the plot of squared correlation coefficients for each patch category are displayed for bird-size categories 3, 4, 5, 6, and 7 (Figure 4-3). From this plot, several of the bird-size categories had "peak" r^2 values at certain patch categories. Category 3 and 5 had peak r^2 values at patch category C. Category 7 had a peak r^2 value at patch category E. The other categories (4 and 6) showed little indication of any peak r^2 values and BPS was not estimated. At 1.5 km^2, these canopy patch categories translate into best patch sizes of 756.0 - 1080.0 m^2 for categories 3 and 5, and 1476.0 - 1800.0 m^2 for category 7. Comparing the upper limits of best patch sizes of each bird-size category, larger birds tended to respond to larger patch sizes (Figure 4-4).

The best patch sizes for birds in category 8 (best prediction area = 25.0 km^2) could not be estimated because the r^2 at each patch category was well below 0.2. This was a result of category 8 birds primarily responding to PCA II, which is a measure of the degree of fragmentation.

Summary: A summary of the best prediction areas, primary responses to structure (e.g., percent cover or degree of fragmentation), and best patch sizes relevant to each bird size category is listed in Table 4-11.

Table 4-9. Squared correlation coefficients (r^2) and standardized partial regression coefficients (*b*) from multiple regression of PCA axes that gave the highest partial regression coefficients at each of the spatial areas during the Spring (PCA I = percent cover; PCA II = degree of fragmentation).

Size Category (g)	r^2	*b* 0.2 km^2 (PCA I)#	*b* 1.5 km^2 (PCA I)#	*b* 85.0 km^2 (PCA II)*
0-6.9	0.116	0.599	-0.205	0.196
7.0-16.5	0.334	0.671	-0.056	0.066
16.6-21.6	0.578	0.144	0.363	-0.306
21.61-33.75	0.568	-0.366	0.7018	-0.41
33.76-61.6	0.713	0.03	0.594	-0.263
61.7-115	0.487	-0.013	0.623	-0.106
115.1-184	0.674	-0.7668	1.373*	-0.134

* P-value and uniqueness index < 0.05

Positive partial regression coefficients indicate that the counts of birds increase with an increase in percent tree canopy cover.
* Positive partial regression coefficients indicate that the counts of birds increase with an increase in the ratio of large to small patches (i.e., less fragmentation).

Table 4-10. Squared correlation coefficient (r^2) and standardized partial regression coefficients (*b*) from multiple regression of PCA axes that gave the highest partial regression coefficients at each of the spatial areas during the Spring (PCA I = percent cover; PCA II = degree of fragmentation).

Size Category (g)	r^2	*b* 0.2 km^2 (PCA I)#	*b* 1.5 km^2 (PCA I)#	*b* 25.0 km^2 (PCA II)*
185.0-576.5	0.571	0.15	0.193	-0.526*

* P-value and uniqueness index < 0.05

Positive partial regression coefficients indicate that the counts of birds increase with an increase in percent tree canopy cover.
* Positive partial regression coefficients indicate that the counts of birds increase with an increase in the ratio of large to small patches (i.e., less fragmentation)

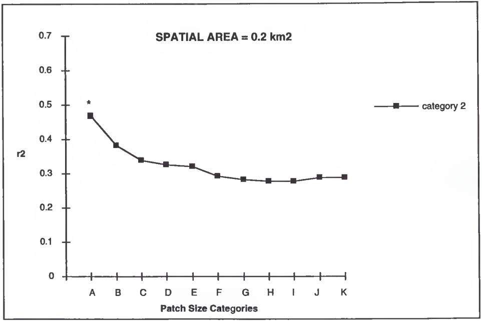


Figure 4-2. Plot of squared correlation coeffecients from simple regressions of counts for bird size category 2 and amount of canopy cover for patch size categories from Spring measurements. An asterisk indicates a "peak" squared correlation coefficient.

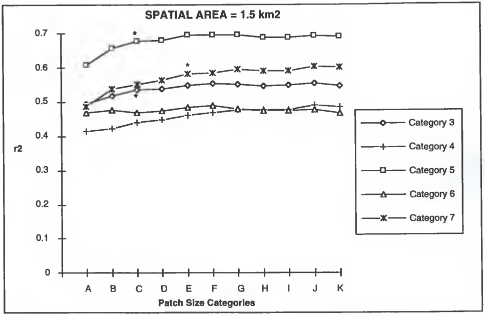


Figure 4-3. Plot of squared correlation coeffecients from simple regressions of counts for each bird-size category and amount of canopy cover for each patch size category from Spring measurements. An asterisk indicates a "peak" squared correlation coefficient. Bird-size categories 3 and 5 have r^2 at patch category C. Bird-size category 7 has a peak r^2 at patch category E.

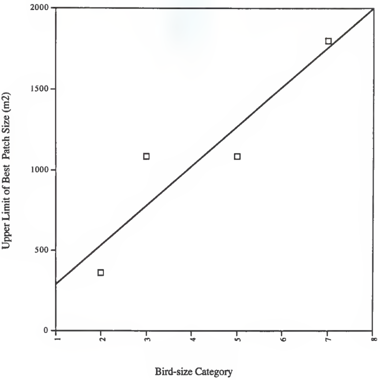


Figure 4-4. A plot of the relationship between bird-size category and the upper limit of best patch size during the spring.

Table 4-11. Summary of how birds respond to canopy cover during the spring season.

Bird Size Category	Size Range (g)	Response at scale of 0.2 km2	Response at scale of 1.5 km2	Response at scale of 25.0 km2	Response at scale of 85.0 km2	Best Prediction Area (km2)	Best Patch Size (m2)
1	0.0 - 6.9	-	-	-	-	-	-
2	7.0 - 16.5	cover +	cover +	-	-	0.2	36.0 - 360.0
3	16.6 - 21.6	cover +	cover +	-	frag +	1.5	756.0 - 1080.0
4	21.61 - 33.75	cover +	cover +	-	frag +	1.5	?
5	33.76 - 61.6	cover +	cover +	-	frag +	1.5	756.0 - 1080.0
6	61.7 - 115.0	cover +	cover +	-	frag +	1.5	?
7	115.1 - 184.0	cover +	cover +	-	frag +	1.5	1476.0 - 1800.0
8	185.0 - 576.5	-	cover +	frag +	-	25.0	-

cover + :More canopy cover results in more birds
cover - : Less canopy cover results in more birds
frag + : More fragmentation results in more birds
frag - : Less fragmentation results in more birds

Summer Surveys: Principle Component Analyses (PCA) and Multiple Regression Analyses

All sites were used in the PCA and subsequent multiple regression analyses for 7 of the 8 bird-size categories; category 8 was analyzed with all of the sites except the Chicago and Blacksburg sites. The Chicago and Blacksburg sites were left out for category 8 because it was believed that the researchers in the Chicago and Blacksburg area did not census the American crow (the main bird in category 8).

PCA results. Across all scales and sites, the first two PCA components explained greater than 97% of the variance in the percent cover of the 11 patch categories. The first PCA component (PCA I) was interpreted as the percent cover axis and reflected a gradient of sites ranging from those with little percent cover by primarily small patches to sites with large percentages of cover by large patches (typically greater than 95% of the variation was explained by PCA I). When two sites had similar total percent cover, the site with a larger percentage of cover by larger patches was given a higher score. The second PCA component (PCA II) was interpreted as a fragmentation axis, sites with a higher small to large object ratio were separated from sites with a lower small to large object ratio (typically less than 5% of the variation was explained by PCA II).

Summer multiple regression results. During the summer, squared correlation coefficients (r^2) were significant at 0.2 km^2 and 1.5 km^2 (values ranged from 0.30 to 0.67) for bird-size categories from 3 to 7; exceptions were category 1 which had no significantly high r^2 values, and categories 2 and 8 which had no r^2 values above 0.3. None of the bird-size categories had relatively high r^2 values at 25.0 km^2 and 85.0 km^2 (Table 4-12). Thus, during the summer breeding season, bird counts in size categories from 3 to 7 correlated with tree canopy cover at 0.2 km^2 and 1.5 km^2, and both category 2 and 8 correlated with tree canopy cover at 0.2 km^2.

Standardized partial regression coefficients (Tables 4-13 & 4-14) indicated that at the nominal scale of 1:2400 (areas of 0.2 km^2 and 1.5 km^2), the bird counts in size categories from 3 to 7 significantly correlated with percent cover (PCA I: *P*-values and uniqueness indices < 0.05). More canopy cover was correlated to more birds. For category 2, standardized partial regression coefficients indicated that at the spatial area of 0.2 km^2, bird counts were significantly correlated with the ratio of small patches to large patches (PCA II: *P*-values and uniqueness indices < 0.05) with percent cover playing a close secondary role ($0.05 < P < 0.15$ for standardized coefficient). Less fragmentation and more cover equaled more birds in category 2. For category 8, standardized partial regression coefficients indicated that at the spatial area of 0.2 km^2, bird counts were significantly correlated with the ratio of small to large patches (PCA II: *P*-value and uniqueness index < 0.05). More fragmentation was correlated with more birds in category 8.

Summer best prediction area (BPA). Multiple regression of the two main PCA components at the nominal scale of 1:2400 (PCA I for 0.2 km^2 and 1.5 km^2) revealed that category 4 had the highest partial regression coefficient at 0.2 km^2 (*P*-value and uniqueness index < 0.05); categories 3, 5, and 6 had the highest partial regression

Table 4-12. Squared correlation coefficients for bird-size categories from multiple regression equations between Summer bird counts (#birds/hr) and percent tree canopy coverage at several different scales. Bold values indicate the highest r^2 among the four spatial areas.

SCALE (area)	BIRD-SIZE CATEGORIES (grams)							
	0.0 to 6.9 (g)	7.0 to 16.5 (g)	16.6 to 21.6 (g)	21.6 to 33.75 (g)	33.76 to 61.6 (g)	61.7 to 115.0 (g)	115.1 to 184.0 (g)	185.0 to 576.5 (g)
0.2 km^2	**0.15***	**0.29***	0.56*	**0.62***	0.54*	0.23*	**0.38***	**0.44***
1.5 km^2	0.04	0.17	**0.66***	0.53*	**0.67***	**0.32***	**0.38***	0.19
25.0 km^2	0.01	0.05	0.29	0.22	0.32	0.02	0.23	0.06
85.0 km^2	0.04	0.04	0.28	0.18	0.23	0.04	0.05	0.19

* P-value < 0.05 (df = 1)

Table 4-13. Standardized partial regression coefficients (*b*) for bird-size categories from multiple regression analyses of Summer bird counts (#birds/hr) and percent tree canopy coverage at 1:2400 (0.2 km^2).

Bird Size (grams)	***b* of PCA I**[1]	***b* of PCA II**[2]
0.0 - 6.9	-	-
7.0 - 16.5	0.2320	0.4850*
16.6 - 21.6	0.7100*	-0.2500
21.61 - 33.75	0.7850*	0.0040
33.76 - 61.6	0.7310*	0.0170
61.7 - 115.0	0.4700*	0.0920
115.1 - 184.0	0.6110*	0.0260
185.0 - 576.5	0.1200	-0.6600*

* P-value and uniqueness index < 0.05

[1] Positive partial regression coefficients indicate that the counts of birds increase with an increase in percent tree canopy cover.

[2] Positive partial regression coefficients indicate that the counts of birds increase with an increase in the ratio of large to small patches (i.e., less fragmentation).

Table 4-14. Standardized partial regression coefficients (*b*) for bird-size categories from multiple regression analyses of Summer bird counts (#birds/hr) and percent tree canopy coverage at 1:2400 (1.5 km^2).

Bird Size (grams)	***b* of PCA I**[1]	***b* of PCA II**[2]
0.0-6.9	0.0002	-0.0200
7.0-16.5	0.2420	-0.3290*
16.6-21.6	0.7890*	0.1900
21.61-33.75	0.7300*	-0.0140
33.76-61.6	0.8170*	-0.0570
61.7-115.0	0.5430*	-0.1700
115.1-184.0	0.6112*	-0.0450
185.0 - 576.5		

* P-value and uniqueness index < 0.05

1 Positive partial regression coefficients indicate that the counts of birds increase with an increase in percent tree canopy cover.
2 Positive partial regression coefficients indicate that the counts of birds increase with an increase in the ratio of large to small patches (i.e., less fragmentation).

Table 4-15. Squared correlation coefficients (r^2) and standardized partial regression coefficients (*b*) from multiple regression of PCA axes that gave the highest partial regression coefficients at each of the spatial areas during the Spring (PCA I = percent cover; PCA II = degree of fragmentation).

Size Category (g)	r^2	*b* 0.2 km^2 (PCA I) *1*	*b* 1.5 km^2 (PCA I) *2*
0.0-6.9	-	-	-
7.0-16.5	-	-	-
16.6-21.6	0.626	0.125	0.681*
21.61-33.75	0.628	0.600*	0.216
33.76-61.6	0.670	0.120	0.714*
61.7-115.0	0.295	0.022	0.524*
115.1-184.0	0.403	0.330	0.320

* P-value and uniqueness index < 0.05

1 Positive partial regression coefficients indicate that the counts of birds increase with an increase in percent tree canopy cover.

2 Positive partial regression coefficients indicate that the counts of birds increase with an increase in the ratio of large to small patches (i.e., less fragmentation).

coefficients at 1.5 km^2 (P-values and uniqueness indices < 0.05); and category 7 had similar partial regression coefficients at 0.2 km^2 and 1.5 km^2 (P-values and uniqueness indices > 0.05) (Table 4-15). For categories 2 and 8, a multiple regression was not needed because these birds had a significant r^2 only at 0.2 km^2. These results indicated that bird counts in categories 2, 4 and 8 correlated primarily with the amount of tree canopy cover at 0.2 km^2; birds in categories 3, 5, and 6 correlated primarily with the amount of tree canopy cover at 1.5 km^2; and bird counts in category 7 had similar correlations with the amount of tree canopy cover at both at 0.2 km^2 and 1.5 km^2. Overall, BPA used by birds to evaluate landscape structure did not increase with body size during the nesting season.

Summer best patch size (BPS). At the spatial area of 0.2 km^2, the plot of correlation coefficients for each patch category are displayed for categories 2, 4, 7 and 8 (Figure 4-5). From this plot, none of the categories showed an indication of peak r^2 values. Thus, best patch sizes were not calculated.

At the spatial area of 1.5 km^2, the plot of correlation coefficients for each patch category are displayed for categories 3, 5, 6 and 7 (Figure 4-6). From this plot, only bird-size category 3 had a peak r^2 value (patch category E). All other bird-size categories showed little indication of peak r^2 values. Thus for bird-size category 3, the best patch size was 1476.0 - 1800.0 m^2.

Summary. A summary of the best prediction areas, primary responses to structure (e.g., percent cover or degree of fragmentation), and best patch sizes relevant to each bird size category is listed in Table 4-16.

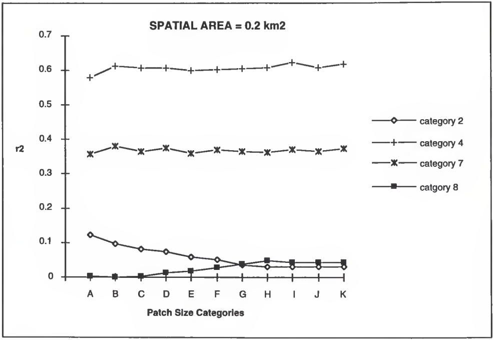


Figure 4-5. Plot of squared correlation coefficients from simple regressions of counts for each bird-size category and amount of canopy cover for patch size categories from Summer measurements.

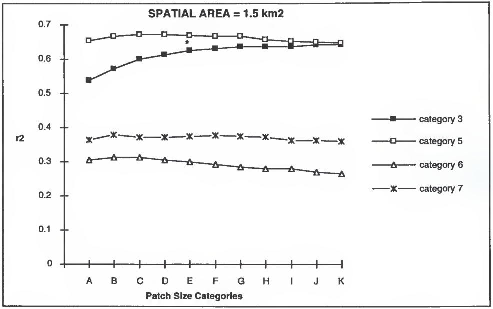


Figure 4-6. Plot of squared correlation coefficients from simple regressions of counts for each bird-size category and amount of canopy cover for patch size categories from Summer measurements. An asterisk indicates a "peak" squared correlation coefficient. Bird-size category 3 has a peak r^2 at patch category E.

Table 4-16. Summary of how birds responded to canopy cover during the summer season.

Bird Size Category	Size Range (g)	Response at scale of 0.2 km2	Response at scale of 1.5 km2	Response at scale of 25.0 km2	Response at scale of 85.0 km2	Best Prediction Area (km2)	Best patch size (m2)
1	0.0 - 6.9	-	-	-	-	-	-
2	7.0 - 16.5	frag - & cover +	cover +	-	-	0.2	?
3	16.6 - 21.6	cover +	cover +	-	-	1.5	1476.0 - 1800.0
4	21.61 - 33.75	cover +	cover +	-	-	0.2	?
5	33.76 - 61.6	cover +	cover +	-	-	1.5	?
6	61.7 - 115.0	cover +	cover +	-	-	1.5	?
7	115.1 - 184.0	cover +	cover +	-	-	0.2 & 1.5	?
8	185.0 - 576.5	frag +	-	-	-	0.2	-

cover + : More canopy cover results in more birds
cover - : Less canopy cover results in more birds
frag + : More fragmentation results in more birds
frag - : Less fragmentation results in more birds

Discussion

Analyses of avian body size clumps were useful in determining the spatial areas and patch sizes relevant to different species when they choose stopover or dispersing sites during the spring and home range areas during the summer. This is not surprising because many ecological, behavioral, and physiological traits are correlated to body size (Peters 1983, Calder 1984, Schmidt-Nielson 1984, Schoener 1968). What is unique about these results is that they allowed the development of actual dimensions for the spatial areas at which birds respond to landscape structure along with the patch sizes sampled by birds. Correlations determined in this chapter are interpreted as the spatial areas and patch sizes used by birds when they "select" habitats. However, because this is the first attempt to address at what large scales different birds are responding to structure, these results should be viewed as hypotheses or guidelines for future research.

Many new insights were ascertained from this study about avian responses to landscape structure and how researchers should conduct research in this area. In the following discussion, I will (1) discuss the trends in the best patch sizes and spatial areas utilized by birds in the spring and summer, (2) discuss how the results relate to avian conservation and metapopulation dynamics, (3) discuss difficulties and possible solutions in studies of the scale(s) at which birds respond to landscape structure, (4) discuss the generality of these results for other avian communities and the practicality of using bird clump structure, and (5) suggest future research in exploring the best patch sizes and spatial areas utilized by birds.

Trends in the Spring and Summer

Best patch sizes (BPS). In the spring, when choosing a stopover/dispersing site, the counts of larger birds tended to be most strongly correlated to larger canopy patches. This trend is consistent with the hypothesis that the sizes of objects utilized by organisms are a function of their body size (Holling 1992b). However, category 1 birds (primarily hummingbirds and kinglets) had no significant correlation to canopy cover at even the smallest patch size (36.0 m^2) in either the spring or summer. The smallest patch size of 36.0 m^2 measured in this study may be too coarse for these small birds; hummingbirds and kinglets may be responding to much finer object sizes such as the sizes and quantities of tree limbs, branches, and even leaves.

Also, it is interesting to note that spring best patch sizes of birds from the smallest to the largest bird-size category seem to be discontinuous. Category 2 birds had the smallest BPS, categories 3 and 5 had equal but medium BPS, and category 7 had the largest BPS. This may be an indication of the "domains of scale" or hierarchical landscape structure in which patterns and processes are quite similar within a domain but different when one moves from one domain to another (Wiens 1989, Holling 1986, Holling 1992, Allen and Starr 1982, O'Neill et al. 1986). Perhaps birds of category 2 respond to structure at a smaller-scale domain, birds of categories

3 to 5 respond to structure at a medium-scale domain, and birds of category 7 respond to structure at a large-scale domain.

Most approaches to detect the hierarchical structure in a landscape have involved measuring patterns in landscapes at different scales. For example, one approach looks for peak variances in some ecological variable, such as patchiness of vegetation (Greig-Smith 1979). As one moves from small to large scales, variance increases as one approaches a transition from one hierarchical level to the next (O'Neill et al. 1986). Another technique uses fractal geometry (Mandelbrot 1983) and looks for breaks in the fractal dimension as an indication of different hierarchical levels (e.g., Krummel et al. 1987). The results of this study suggest that the BPS of birds may track hierarchical landscape structure. Perhaps, birds in different size categories respond to structure at different hierarchical levels.

Summer best patch sizes could only be calculated for one bird-size category (#3). Birds of category 3 had a larger BPS in the summer than during the spring. Other bird-size categories may have similar increases in BPS, but I could not detect it in this study because the sizes of canopy patches may not have been variable enough (see section below on problems with measuring the scales relevant to avian species). If this were so, birds may respond to larger patches of canopy cover during the breeding season, as compared to the spring migration season. This may be due to increased resource demand during the nesting period. Most organisms have some sort of dispersal phase and an organism's response to landscape structure may be quite different during its dispersal phase than during its sedentary phase (Levins 1992, Wiens 1976). Highly vagile species may perceive spatial patterns in a landscape at different scales than more sedentary species (Kosala and Rollo 1991). Thus, when birds are migrating across the landscape during the spring, they are primarily in a foraging mode and may be responding to smaller patches because opportunities to feed in these patches exist. In contrast, when birds are searching for a nesting area during the summer, they are searching primarily for appropriate nesting areas and only large patches are suitable for nesting.

Best prediction area (BPA). During the spring, counts of larger birds tended to be primarily correlated with the amount of tree canopy cover at larger spatial areas (category 2 = 0.2 km^2; category 3, 4, 5, 6, and 7 = 1.5 km^2; category 8 = 25.0 km^2). This is consistent with the hypothesis that larger birds would respond primarily to structure within larger spatial areas than smaller birds and is somewhat analogous to the observation that larger birds have larger home ranges (Schoener 1968).

During the summer, results were not so consistent with the hypothesis that larger birds respond to structure at larger spatial areas (category 2, 4, & 8 = 0.2 km^2; 3, 5, 6, & 7 = 1.5 km^2). An alternative explanation is that while object size, which organisms sample in a landscape, is directly correlated to body size, the size of a spatial area (e.g., home range) is dependent on trophic status, food type, and productivity in a landscape (Haerstad and Bunnell 1979, Holling 1992b). Therefore, a possible reason that bird counts in category 2, 4 and 8 were correlated with structure within the same spatial area is that the resources used by these birds are distributed in a similar-sized area. However, for category 8 birds, 0.2 km^2 is probably too small of an area used by these birds to select home ranges. Probably, the way I measured canopy structure did not represent the way category 8 birds measure structure at the larger spatial areas (see below: problems with measuring the scales relevant to avian species).

Comparing the spring and summer results, birds during the spring respond to structure at a much wider range of scales than during the summer. The presence of a bird in a particular area during the spring may be due (at least in part) to the distribution of canopy cover within a 85.0 km^2 area. However, during the summer, the distribution of canopy cover within a 85.0 km^2 area does not really play a role in the selection of a breeding home range by the birds recorded in this study.

Finally, in both the spring and summer, category 1 birds did not respond to the variation in tree canopy cover at any of the four spatial areas; thus best prediction area could not be evaluated. Of course, one possible explanation for this is that these birds are not responding to the measured variable of tree canopy cover; they could be responding to some other textural attribute such as the distribution of small bushes, flowers, or some type of understory vegetation. Another explanation is that the smallest spatial area used in my analyses was still too large. An average territory size for rufous hummingbirds (*Selasphorus rufus*) is around 0.0004 km^2 (maximum 0.0014 km^2) (Gass 1979). Thus, 0.2 km^2 is much too large for measuring structure relevant to these birds when they are choosing home ranges or stopover/dispersal sites. If I had known specifically where the hummingbirds and kinglets were sampled along a survey transect, then I could have measured the tree canopy cover within a much smaller spatial area.

Canopy cover and fragmentation. Birds in each of the categories responded to either the amount of canopy cover or to the degree of fragmentation. During the spring, categories 2 to 7 responded primarily to the amount of cover at 0.2 km^2 and 1.5 km^2 (more cover = more birds). This response of categories 2 to 7 is consistent with the notion that more structure will attract more birds (Cody 1985). Category 8 birds responded primarily to fragmentation at 25.0 km^2 (more fragmentation = more birds) and to the amount of cover at 1.5 km^2 (more cover = more birds). This makes sense because birds in this category (e.g., band-tailed pigeons, northwestern crows, and American crows) use tree canopy to roost and sometimes to forage, but much of their foraging activity occurs on the ground (Ehrlich et al. 1988). During the spring migration season, perhaps these birds are primarily "choosing" 25.0 km^2 areas with lots of scattered tree patches and open foraging areas; percent cover and size of patches has a secondary importance at 25.0 km^2 but may play a role at 1.5 km^2. At the scale of 85.0 km^2, more canopy fragments in a landscape resulted in more birds sighted in suburban censuses for size categories 3, 4, 5, and 7. Birds probably are not attracted to canopy fragments, but single large patches in a 85.0 km^2 landscape matrix may be a strong attractor for migrating birds. Sites embedded in this matrix would have fewer birds than similar sites embedded in a more fragmented landscape.

During the summer, though, a different picture emerged at least for category 2 birds. At 0.2 km^2, category 2 birds responded primarily to the degree of fragmentation (less fragmentation = more birds) and somewhat to percent cover (more cover = more birds). This response is consistent with how some of the smaller birds in this category respond to forest fragmentation. Many of the vireos and warblers have been shown to be area and edge sensitive, breeding in large areas of continuous forest and avoiding edges (Freemark and Collins 1992, Robbins et al. 1989). Thus, birds of this size category may be searching for landscapes with less edge and more canopy cover at the scale of 0.2 km^2. Birds in categories 3 to 7 responded primarily to the amount of canopy cover at the scale of 0.2 km^2 and 1.5 km^2 (more cover = more birds); this is consistent with the notion that more structure would attract more birds. Category 8 birds responded primarily to the degree of fragmentation at the scale of 0.2 km^2 (more fragmentation = more birds), and as mentioned earlier, this is probably related to the ground foraging behavior of these birds. Lots of scattered trees provide nesting sites whereas open areas in between these trees provide foraging sites.

Avian Conservation and Metapopulation Dynamics

As expressed earlier, many researchers in ecology recognize the need to determine the scales relevant to an organism to understand many ecological phenomena (Levins 1992, Wiens 1989, Lima and Zollner 1996). For example, the way species respond to landscape structure at various scales can influence ecological communities through competitive interactions (Hanski 1995) and predator-prey dynamics (Hengeveld 1987). Determining species-specific responses to landscapes also have many applications to conservation biology (see review by Arnold 1995). For example, how much of a forest can be removed before an interior-forest specialist perceives a forest as unsuitable for nesting? How much of a forest fragment can be developed before migrating species stop using it as a stopover site? How can one design a network of patches that promote the dispersal of a species from one habitat patch to another? All of these questions depend upon determining the spatial areas and patch sizes relevant to a targeted species.

In this study, it seems that birds respond to canopy patches of smaller sizes within a smaller range of spatial areas when migrating/dispersing than when nesting; thus patterns in the landscape would have different effects during these two seasons. These differences have implications for the conservation of many bird species. For example, approximately two-thirds of the breeding bird species of eastern United States migrate to Mexico, Central America, and South America (Keast and Morton 1980, Terborgh 1992, Rappole 1995). Mortality during migration is probably high (Moreau 1972, Ketterson and Nolan 1982, DeGraaf and Rappole 1995) and birds will forage in stopover sites that provide many critical resources such as food, protection from predators, and shelter from adverse weather (Moore and Simons 1992, Lindstrom 1990, Winker et al. 1992a). Not much is known about the stopover ecology of migrants (Moore 1980, Winker et al. 1992b, Rappole 1995), and nothing is known about the spatial area and patch size utilized by migrating birds when choosing stopover sites. Most of the studies have looked at the types of habitats preferred by migrants, such as a study by Moore et al. (1990) which found that migrants preferred scrub-shrub and forest habitats on the northern coast of the Gulf of Mexico. However, the spatial pattern of these habitats at different scales was not addressed and this scale-dependent pattern would be a deciding factor on whether migrants use a particular stopover site. The results from this study indicate that migrants may use even highly fragmented suburban landscapes. Many suburban sites probably lie along flyways, and an increased number of suitable foraging habitats in these suburban areas could promote the survival of a number of migrants during the migration season.

In terms of short distance dispersal, the pattern of landscape structure and the way birds respond to this structure will promote or constrain avian species from moving from one area to the next. Most animal species display a wide variety of dispersal patterns and distances (Wiens et al. 1976). The probability of movement across a landscape matrix has been used in many metapopulation models and studies of animal population dynamics within a region (Hanski 1991, Fahrig and Paloheimo 1988, Opdam 1990, Stenseth and Hansson 1981, Stacey and Taper 1992). But models frequently use simple rules of movement and patch choice (e.g., Fahrig 1988), and incorporation of empirically based, species-specific habitat selection and movement at large scales is virtually nonexistent (Dunning et al. 1995, Lima and Zollner 1996). The effect of the landscape matrix on the ability of organisms to disperse from one area to the next will depend on the sizes of objects that a species responds to within a given area (Kremaster & Bunnell 1992, Wiens 1995, Wiens et al.

1976). In this study, category 3 birds responded to smaller patches in a landscape when dispersing than when nesting; thus, landscapes that may not be useful for breeding may be useful for dispersing between breeding habitats. Again, the results of this study suggest guidelines for the sizes of patches within a given spatial area that would attract birds of different sizes. Appropriate breeding habitats connected by a network of dispersal-friendly habitats would promote the health of a regional metapopulation.

In summary, when humans alter a landscape, the way animals respond to remnant landscape structure will determine the extinction from a region or the disappearance of a species from a local area. Fragmentation of a landscape at specific scales will affect different sizes of animals in markedly different ways (Harris 1984). For example, Morton (1990) proposed that the extinction of many middle-sized Australian mammals was due to how these mammals responded to fragmented landscapes; their response was a function of their size. Changed fire regimes and the introduction of rabbits caused the distribution of productive patches to become smaller and smaller and to be spaced farther and farther apart in Australian landscapes. Small animals, responding to small patch sizes, could still find enough resources in the remaining small patches whereas large animals, responding to large patch sizes, had an ambit large enough to travel between the patches. Essentially, large animals utilized clusters of small patches as one big patch. Middle-sized animals, responding to medium patch sizes, went extinct because they could neither find enough resources in each small patch nor travel between patches. Thus, knowing the relevant spatial areas and patch sizes of different species is critical to understanding how the scale-dependent impact on a landscape would affect animals.

Problems with Measuring the Scales Relevant to Avian Species

Researchers have long recognized that scale is an important variable in many ecological studies (Allen and Starr 1982, Addicot et al. 1987, Meentemeyer and Box 1987, O'Neill et al. 1986). Landscape pattern changes at different scales, and the appropriate scale to answer questions about the ecology of animals is dependent on the range of scales relevant to each species (Levins 1992, Turner et al. 1989, Wiens 1989b, Wiens et al. 1993, Wiens 1995, Haila 1991). However, what are the relevant scales for avian species as well as other species? To date, the scale of analysis for most ecological studies has been rather arbitrary (Wiens 1989, Lima and Zollner 1996).

This study attempted to determine the appropriate spatial areas and patch sizes used by different sizes of birds when choosing home ranges, stopover sites, and dispersing sites. Although the results of this study led to the development of many new hypotheses about the spatial areas and patch sizes used by different bird species, I encountered some difficulties in measuring landscape structure and analyzing/interpreting the correlation of landscape data with bird densities. In the following discussion, I will present several problems researchers will have when attempting to discover the scales relevant to birds. The problems fall into three categories: (1) measuring landscape structure from aerial photographs at different scales, (2) determining the best patch size of different bird species in patchy landscapes, and (3) relating human-biased measurements of the landscape to avian perceptions of the landscape.

(1) Any aerial photograph is defined both by its spatial area (or window size) and its resolution (or pixel size). The decision of an animal to locate itself in an area also is defined by the spatial area it uses to evaluate information in an environment and by the sizes of objects responded to by an animal (Holling 1992, Wiens 1990). However, the spatial area and resolution of an aerial photograph may not be appropriate to use when determining the spatial area and patch size that animals use to evaluate landscape structure. Aerial photos taken at high altitudes cover large spatial areas, but the resolution of an aerial photo decreases and small objects in the photo disappear along with groups of small objects fusing into one object. In part, the pattern in the landscape changes as a function of a photo's resolution. For larger birds in this study, the spatial area used to evaluate landscape structure may be quite large. However, the size of objects responded to by these large birds may be much smaller than the resolution of typical high-aerial photographs. This might have been the case with category 8 birds during the summer where larger spatial areas failed to reveal high squared correlation coefficients. It could be that these large birds choose home range areas based on the number of small patches distributed over a large spatial area. Aerial photos at the larger nominal scales (e.g., 1:24,000 & 1:40,000) would not detect these small patch distributions. The only way to remedy this situation would be to piece together a number of aerial photos taken at the nominal scale of 1:2400, with enough photos to represent a large spatial area (e.g., 25.0 km^2).

(2) Comparing the densities of birds that use different landscapes proved to be difficult in terms of estimating the best patch size (BPS) of different species. To determine the BPS of birds in different body-size categories, I ran separate regressions between bird densities and 11 different patch size categories that ranged from percent cover of the smallest canopy patches to percent cover of the largest patches. However, there was a high degree of correlation between percent cover and patch sizes in a landscape; typically, landscapes with large patch sizes also had the largest amount of cover at all patch size categories. This is because large patches also contained lots of small patches, and the differences in percent cover among the sites were not that variable from one patch size category to the next. Thus, some bird-size categories did not have a definitive "peak" r^2 in the analyses because the canopy patch sizes used by birds in a particular bird category were not variable enough (see Figure 4-7). A few bird-size categories did have "peak" squared correlation coefficients at certain patch size categories and BPS could be evaluated. Although these "peak" r^2s were not dramatic, I argue that these peak values are real because percent cover among the sites was not that variable from one patch size category to the next. Also, because the patch-size categories were not independent of each other, squared correlation coefficients tended to be similar. Any peak correlation coefficient is probably a good indication of the BPS of birds in a body- size category.

This above situation is probably common for any study that compares the spatial geometry of several different landscapes to determine the best patch size of birds. The best way to determine

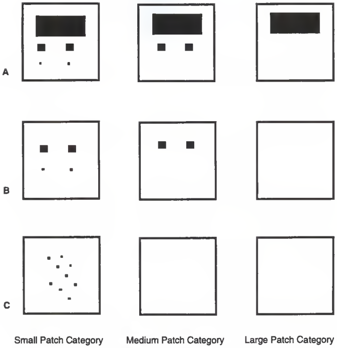


Figure 4-7. The above images represent three hypothetical areas where birds were censused. Site A contained the highest density of birds, B the next highest, and site C had the lowest density. Site A had the largest percent percent cover at the small patch category whereas sites B & C had equal percent cover. The percent difference in canopy cover between sites A & B from the small patch category to the large patch category is somewhat constant. Thus, simple regressions between percent cover and bird density at each patch category would result in similar correlation coefficients. However, comparing sites B & C, the percent cover between the two sites is equal at the small patch category but changes at the medium patch category. Thus, a regression between sites B & C would result in a "peak " correlation coefficient at the medium patch category.

the BPS of birds is to compare the densities of birds in several different sites where the percent cover of structure, at a relevant spatial area, is similar but the geometry is totally different. For example, one site could be comprised of two large patches, another site could be comprised of 20 medium patches, and a third site could be comprised of 100 small patches; the commonality among the sites is that the percent cover is exactly the same. An analysis of the bird densities among these distinct sites would reveal the BPS used by birds of different sizes.

(3) Another potential problem with determining the best prediction area (BPA) and best patch size (BPS) relevant to birds has to do with how measurements of landscape structure is biased by the human eye. My measurements of canopy cover could not account for the possibility that clusters of canopy patches (at a spatial area) may actually be the structure that birds sample (Figure 4-8). If one were to "blur" an image to a point where clusters become whole patches, then the analyses might show that the BPS may be much larger for some species than revealed by conventional analyses. This is especially true for larger birds that have larger ambits. An aerial photograph with a lot of small, scattered patches may look like this to our eye, but to birds with large ambits, the clusters of scattered patches may be several big patches (hence patch size) that are usable by these birds. This most likely was the case with the category 8 birds during the spring season. Analyses revealed that counts of large birds correlated with sites that had lots of small canopy patches (at 25.0 km^2). These birds, though, were probably responding to

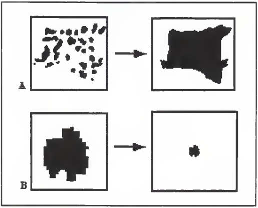


Figure 4-8. Representation of two possible perceptions of the landscape by birds: A) a group of patches that actually are viewed as one big patch, and B) one big patch that actually is viewed as one little patch.

clusters of small patches. Holling (1992) described such a situation where aggregates of individual objects in a landscape essentially fuse into patches at larger scales, and he proposed that large animals with large ambits could exploit this landscape. This is an important concept considering that patterns in a landscape may be viewed by birds differently than the way researchers measure it.

Along these lines, another problem with correlating patches of landscape with bird counts is the possibility that certain birds may be responding to microhabitats within a relatively large patch (Figure 4-8). This would lead to difficulties in estimating the "true" patch size because measurements of landscape structure is again based on what our eye can see in an aerial photograph. For example, during the summer breeding season, this certainly may be the case of interior forest specialists that use small patches of forest embedded in large remnants of forest (Robbins et al. 1989). My analyses would overestimate the BPS of these birds because these small birds would be correlated to the number of large patches in a landscape. When one compares the calculated BPS of small interior forest specialists to that of larger birds, it would seem that smaller and larger birds had a similar BPS when in fact the "true" BPS of the small birds is much smaller.

Bird Clump Analyses and Generalizations to Other Avian Communities

Ecological systems to the human eye seem extraordinarily complex (Holling 1987), and it is a daunting task for ecologists to understand and measure ecological phenomena across multiple scales. This is especially true when trying to determine the scales at which landscape structure is relevant to birds. Bird clump analyses simplify the task of determining the spatial areas and patch sizes relevant to each species by grouping species into size categories; each category represents a suite of birds responding to landscape structure within the same range of scales (Holling 1992b). Of course, the underlying assumption is that body size dictates the range of objects perceived by an organism; this is probably a reasonable assumption because many ecological and behavioral variables are correlated with body size (Brown 1995, Calder 1984). Body size should be useful in approximating the range of scales relevant to organisms (Wiens 1989).

The hypothesis that animals respond to a range of objects in a landscape as a function of their body size is intuitive to any researcher that has observed the foraging behaviors of animals in the wild. For example, small birds (e.g., warblers and vireos) forage for food in and around small twigs and individual leaves whereas larger birds (e.g., yellow-billed cuckoos and brown thrashers) ignore these fine textures and concentrate on large branches and patches of leaves. Further, the size range of objects that animals encounter as they move across a landscape is also a function of their size. Imagine a small vole versus a bobcat moving across a 30.0 m^2 patch of landscape. The vole's path is much more tortuous than the bobcat's path because the vole encounters many more physical barriers than the bobcat. In one experiment with grasshoppers, the movement patterns of different sizes of grasshoppers were analyzed as they moved across a grassland mosaic (With 1994). The smaller species followed a much more tortuous path and moved significantly slower than the larger species, indicating that the smaller species was responding to much finer textures in the environment. In summary, the size of an organism is probably a good indicator of the sizes of objects that it responds to in an environment.

Once the BPS used by birds of certain body-size category are estimated at a given scale, these estimates can be used to approximate the BPS of any bird species of similar body sizes. A wide variety of objects can be found at each scale in a landscape, and birds have developed a wide variety of natural life history strategies to exploit objects at each scale. Birds of different foraging strategies may be exploiting qualitatively different structures in an environment, but the sizes of these objects between two similar-sized species should, theoretically, be equal. For example, an arboreal bird forager exploits tree needles and leaves (small objects), individual trees (medium objects), and patches of trees (large objects). A similar-sized ground forager exploits grasses (small objects), patches of grasses (medium objects), and large meadows (large objects). Both birds are measuring the same sizes of objects, but the objects are qualitatively different. An indication of this possibility of markedly different species evaluating the landscape in similar ways comes from a study on the effects of isolation and area on the diversity of marshland birds. Brown and Dinsmore (1986) found that many marshland species did not occur in marshes smaller than 5 ha, a finding similar to that of Opdam (1991) in which many forest-interior birds were absent from woodlots less than 5 ha. Thus, a researcher with a good knowledge of the natural history characteristics of a species can approximate its scale-dependent structural requirements by using the calculated BPS of another species of a similar size.

This is also somewhat true of the best prediction areas (BPA) at which birds respond to landscape structure. A BPA estimate for one species probably represents the BPA of another species of the same size. However, a BPA of an organism may be quite variable depending on the trophic status of the species, its diet, and the productivity in a landscape in which the species occurs. These factors were shown to influence the home range area of many species (Haerstad and Bunnell 1979). Thus, special attention must be given to comparing the BPA of different species of similar sizes.

Further, if BPS and BPA that birds use to evaluate landscape structure (At large scales) were determined for birds in each of the size categories, then researchers (e.g., landscape managers, city planners, wildlife conservationists, and restoration ecologists) would have a tool that could be used to evaluate how landscape changes affect birds and possible ways to restore features in the landscape to attract a greater variety of avian species. Decisions made by birds to locate in an area are probably governed by decisions made at larger scales, more so than at smaller scales. For example, a bird may be known to forage in tree canopy, but one tree may not be enough to attract this species. It probably depends on the number of trees that are distributed at larger scales. If researchers knew the BPS and BPA of birds at large scales, researchers could look at landscape structure in aerial photos in terms of how birds approximately "view" this landscape. This is very practical because currently researchers do not have a firm grasp on the scale-dependent decisions made by birds. Many land-management decisions are based on the rather simple policies of "more is better" or "fragmentation is bad", and these policies are normally biased by human perceptions of landscape structure. In addition, many researchers want to know what types of birds are in a given area and it takes time and money to census these areas. By analyzing the sizes of landscape structure at a range of scales relevant to the organism in question, researchers may be able to approximate the types of species in a given area in a relatively short period of time.

A word of caution should be expressed about interpreting the suitability of a landscape by the presence of a species, especially during the summer breeding season. The presence of a species may indicate that the configuration of the landscape is conducive to attracting this species, but this does not necessarily mean it is reproducing or foraging successfully in this area. A whole host of studies have shown that birds in small woodlots may be prone to nest predators (Wilcove 1985, Small and Hunter 1988). Another factor is that vegetation in some habitats, such as suburban habitats, may consist of mainly exotic plants that contain little usable resources. Birds using these areas may not find sufficient resources to nest or to migrate if the area was used as a stopover site. Also, the abundance of competitors in an area may be artificially high and this would reduce the success of certain bird species (e.g., the abundance of starlings in suburban habitats would decrease nesting success of woodpeckers because starlings are cavity nesters). In essence, the landscape structure may attract certain species, but some areas may actually have become "sinks" with a very low reproductive output or survival rate.

Future Research on Determining Scales Relevant to Avian Species

To better understand the scales at which avian species respond to structure, I recommend the methodological approach as described in this chapter. Analyses should be expanded to include species with different natural life history characteristics (e.g., ground foragers and marsh species) and to include avian communities in many different types of landscapes (e.g., arid environments, estuaries, savannahs, and rain forests). One should pay careful attention to the species (especially trophic status) included in a study and to the level of the decision hierarchy that the study focuses on. In this chapter, the smallest scale (0.2 km^2) was above the home range level of most of the birds used in analyses. If I had included some of the larger hawks, 0.2 km^2 would actually have been a habitat patch within a hawk's home range. For example, a red-tailed hawk, *Buteo jamaicensis*, has a home range of 4.24 km^2 (Schoener 1968). At 0.2 km^2, a correlation between bird counts and the amount of canopy cover would be interpreted as the amount of cover needed to attract a hawk within its home range (not the amount of cover needed for a hawk to "choose" its home range area).

The results of my research have set some initial "boundaries" on how different sizes of birds respond to landscape structure at large scales; however, I suspect that many of my results need to be refined. We have a good idea of the spatial areas and patch sizes birds use to select home ranges, stopover sites, and dispersing sites, but it is premature to state the exact spatial area or best patch size. Future research should analyze structure within a range of spatial areas starting from the best prediction area (proposed in this study) and extending the window size to smaller and larger spatial areas. Where correlations are the highest is probably a good indication of the approximate spatial area most relevant to a birds of a certain size. Once the spatial areas are determined, the best object sizes that birds respond to in an environment should be examined. As mentioned earlier, the best way to determine best patch sizes is to compare sites with different sizes of pertinent landscape objects but with the same total percent cover.

Data would most readily come from published sources; a variety of research programs have censused birds for a variety of reasons and the results of these censuses could be adapted to multi-scale comparisons of landscape structure with bird densities. Another approach would be to choose locations, from aerial photographs, that had the desired spatial geometric features. This would greatly enhance the ability to detect specific best patch sizes of birds because one could choose sites that contained different sizes of objects but had the same percentages of cover. As a third approach, experimental manipulations of landscape structure would be a good way to get at the scale-dependent perceptions of birds. However, I would not recommend this because birds in manipulated areas may display site tenacity, especially during the breeding season, and it may take many years before an effect is noticed. Wiens et al. (1986) tried this landscape manipulation with shrubsteppe birds and found that there was no effect over a five year period; they cautioned researchers from using this type of approach. Also, the level of manipulation would be quite large for larger species and would probably be impractical.

Summary and Conclusions

The results of this study indicate that organizing birds into avian body-size clumps and measuring structure at several different scales were quite useful in exploring how birds respond to scale-dependent structure. Most of the birds in the size categories were responsive to variations of tree canopy cover at several different spatial areas and the best patch sizes for birds in several size categories were calculated. The primary usefulness of this study was discovering difficulties researchers face when they attempt empirically to determine spatial areas and best patch sizes birds use to choose home ranges, stopover sites, and dispersing sites. The recommendations outlined in this chapter will guide future research in this area. Nevertheless, some general trends and specific hypotheses about how birds respond to scale-dependent landscape structure were developed. They are as follows:

Trends

(1) Counts of larger birds tended to be correlated to larger patch sizes and also to patches within larger spatial areas (at least during the spring).

(2) Bird counts were correlated with smaller patch sizes during the spring than during the summer.

(3) Bird counts were correlated with the distribution of canopy patches at larger spatial areas during the spring than during the summer.

Hypotheses

(1) For category 1 birds, the best prediction area is below 0.2 km^2.

(2) For category 2 birds, the best prediction area during the spring is approximately 0.2 km^2 (best patch size = 36.0 - 360.0 m^2) and approximately 0.2 km^2 (best patch size = ?) during the summer.

(3) For category 3 birds, the best prediction area during the spring is approximately 1.5 km^2 (best patch size = 756.0 - 1080.0 m^2) and approximately 1.5 km^2 (best patch size = 1476.0 - 1800.0 m^2) during the summer.

(4) For category 4 birds, the best prediction area during the spring is approximately 1.5 km^2 (best patch size = ?) and approximately 0.2 km^2 (best patch size = ?) during the summer.

(5) For category 5 birds, the best prediction area during the spring is approximately 1.5 km^2 (best patch size 756.0 = 1080.0 m^2) and approximately 1.5 km^2 (best patch size = ?) during the summer.

(6) For category 6 birds, the best prediction area during the spring is approximately 1.5 km^2

(best patch size = ?) and approximately 1.5 km^2 (best patch size = ?) during the summer.

(7) For category 7 birds, the best prediction area during the spring is approximately 1.5 km^2 (best patch size = 1476.0 - 1800.0 m^2) and approximately 0.2 km^2 (best patch size = ?) and 1.5 km^2 (best patch size = ?) during the summer.

(8) For category 8 birds, the best prediction area during the spring is 25.0 km^2 (best patch size = ?) but best prediction area and best patch size were not determined for the summer.

CHAPTER 5

AVIAN BODY-SIZE CLUMPS AND THE IMPACT OF SUBURBAN LANDSCAPES ON AVIAN COMMUNITIES: A SYNTHESIS

Introduction

Humans have become such a dominant force in nature that they can affect ecosystems from very small scales to very large scales (see review in McDonnell and Pickett 1993, Turner et al. 1990). Air, soil, and water pollution, habitat destruction, and introduction of exotics have dramatically changed the structure and function of ecosystems. In fact, some of these effects are operating at the global scale (e.g. global warming) and others are operating at such a large scale (e.g., habitat destruction) that vast regions are being transformed within a relatively short period of time. It is difficult, if not impossible, to find a natural area that has not been affected by humans sometime in the past (Williams 1993). Human-mediated changes in the structure and function of ecosystems, in turn, affect the abundance and diversity of organisms. An integral part of ecology is the study of the factors that influence the abundance and distribution of organisms. Many ecologists have studied the effects of human-modified environments on organisms, but for a variety of reasons, suburban/urban environments have historically been ignored (Cairns 1988, Ludwig 1989, McDonnell et al. 1993).

Suburban areas have a huge impact on the diversity and abundance of many organisms, especially North American birds. A fraction of the native N. American bird species seem to flourish in suburban environments (Geis 1974, Emlen 1974, and Guth 1980). Recent studies on suburban environments stress that habitat structure is the primary factor that determines bird diversity (Penland 1984, Horak 1986, Sexton 1987, Baines 1988, and Stenberg 1988). Habitat structure in suburban landscapes has been fragmented at a variety of scales, but the spatial distribution of landscape structure at large scales is probably a primary predictor of avian diversity and abundance. However, few studies have looked at how birds respond to fragmentation at large scales. Chapter 4 explored how large-scale landscape structure affects different sizes of birds, and the results of chapter 4 indicated that birds do respond to structure at large scales. Together, chapters 2, 3 and 4 also showed how avian body-size clumps could be used to estimate what large-scale structure is relevant to different sizes of birds. The main goal of this is chapter is to summarize how the results of chapters 2, 3, and 4 can be used to study the effects of large-scale landscape structure on the abundance and diversity of avian communities in suburban environments.

I divide this chapter into two sections. I first give an overview of why suburban environments are important to the future survival of birds, and I summarize some of the studies that have been done on avifauna in suburban environments. Then, I outline how avian body-size clumps can be used to estimate the large-scale structure relevant to birds in suburban environments.

Avifauna Studies in Suburban Environments

Suburban environments are becoming, if not already, a dominant landscape type in North America. The expansion of urban cities (i.e., urban sprawl) is quite rapid; the rate that lands are converted to urban use has been estimated to exceed population growth by a factor of six to ten (Richmond 1996). Over one million acres are converted to suburban areas each year (Strohm 1974), and with population growth disproportionally increasing in certain regions of North America, many regions are dominated by a suburban landscape matrix. For example, Florida's human population increases by approximately 650 people per day (Smith and Bayya 1993), and 100,000 hectares of forest are cleared annually to make room for development (Edwards 1988). Many homeowners prefer to live in the suburbs, which ultimately increases the rate of urban sprawl. One noteworthy group, the "baby-boomers", have an estimated one trillion dollars to spend on retirement (Towne 1994), and they want to buy land outside urban city centers. The end result of urban sprawl is the loss of wildlife habitat and the fragmentation of vast regions of North American landscapes.

Suburban landscapes are a patchy mosaic of trees, bushes, lawns, buildings, and roads. The spatial distribution of these patches is quite variable among different cities or within different areas within a city, depending on the local history of development. Economic, political, and social forces that shape development ultimately determine the patchiness of a suburban landscape. Many of the natural features of a suburban environment have been removed and replaced with artificial structures (e.g., buildings, parking lots, and lawns); as a result, the natural habitat structure that remains is quite fragmented. Landscape fragmentation combined with habitat loss has long been known to reduce avian diversity because it decreases the amount of habitat available to birds (e.g., Cody 1985). A bird's decision to abandon or stay in a suburban area is probably based on some rule-of-thumb that concentrates on the size, the quantity, and the distances between landscape objects at different scales in an environment. How humans have modified a landscape plays a critical role in determining the abundance and diversity of birds in suburban environments.

In addition to the effects on avian communities within the boundaries of suburban areas, suburban landscapes may affect the regional distribution and population dynamics of avifauna. Island biogeography theory (MacArthur and Wilson 1967) and the subsequent development of metapopulation theory (Gilpin and Hanski 1991) address the potential effects of large-scale landscape structure on local and regional animal population dynamics. When animals are dispersing from one habitat patch to another, how animals respond to the landscape matrix that exists between habitats is vital to the ability of certain animals to disperse (Harris 1984, Fahrig and Paloheimo 1988, Opdam 1990, Hanski 1991). This dispersal ability may be important to the viability of species in a region (Gilpin and Hanski 1991, Burkey 1989, Stacey and Taper 1992). Suburban landscapes are scattered throughout N. America, and these environments may actually be a barrier to dispersal, depending on how certain species respond to remnant landscape structure in these areas. Furthermore, many suburban environments lie along major migratory routes, and these suburban sites could serve as stopover sites. Mortality during migration is probably high (Moreau 1972, Ketterson and Nolan 1982) and birds need to forage in stopover sites along migratory routes (Moore and Simons 1992). Because of the abundance of suburban areas, preserving sufficient numbers of suburban stopover sites from northern regions to southern regions may play a pivotal role in promoting the survival of migrating birds.

Despite the potential importance of suburban areas to avian communities, ecological studies of bird avifauna in suburban environments have been limited (Pitelka 1942, Emlen 1974). However, several researchers conducted studies on birds in suburban environments (Emlen 1974, Guth 1980, Blair 1996, Wolfenden and Rohwer 1969, Penland 1984, Erz 1966, Sexton 1987, Degraaf 1987). Several researchers have reported higher bird densities in suburban areas than in natural areas, but bird diversity decreased as the degree of urbanization increased (e.g., Blair 1996, Wolfenden and Rohwer 1969, Walcott 1974, Degraaf 1981, although see Emlen 1974). In general, the effects of urbanization include a loss of ground nesters and of canopy/open-nesting species, a dominance of omnivores and ground foragers, and a high density of exotic birds (e.g., house sparrows, starlings, and rock doves). In addition to studying suburban avian abundance and diversity, suburban environments have also been used to study other ecological principles (e.g., McDonnell and Pickett 1993). Several studies have used suburban avifauna to study aspects of community and behavioral ecology, such as the effects of biotic and abiotic factors on avian community structure (Emlen 1974, Sexton 1984, Guth 1980); niche shifts of birds in urban versus natural settings (Walter and Demartis 1972); the effects of predation and competition on avian reproductive success (Woolfenden and Rohwer 1969, Wilcove 1985); and the foraging patterns of suburban birds (Weber 1972, Sexton 1987).

However, a majority of avifauna studies in suburban environments concentrated on how the habitat structure affects the abundance and diversity of birds (e.g., Penland 1984, Horak 1986, Sexton 1987, Baines 1988, and Stenberg 1988, Blair 1996, Emlen 1974, Mills et al. 1989). Generally, researchers measured a variety of vegetative variables along a survey route to ascertain which variable(s) best explained the variation in bird density. These studies were all conducted at small scales (e.g., what percent of tree canopy cover was present within 30.0 meters on either side of a survey transect). Variation in suburban bird densities, though, may best be explained by the spatial distribution of structure at larger scales (as the results of Chapter 4 suggest). Thus, to attract certain bird species to a given area, one must also know the large-scale spatial geometry relevant to different species of birds.

Avian Body-Size Clump Structure and Suburban Landscapes

Chapters 2, 3, and 4 indicate that avian body-size clump structure could be used to measure significant ecological changes in suburban environments. The main utility is that body-size clump structure provides a framework for researchers to conduct future research on how large-scale changes in the landscape affect different sizes of birds. Below, I summarize some of the useful aspects of avian body-size clumps and how the results of chapters 2, 3, and 4 can be used for future research. I also summarize some of the pitfalls of using avian body-size clumps in correlation analyses to ascertain the type of scale-dependent structure relevant to birds in different body-size clumps.

The utility of avian body-size clump structure. First, how different species of birds respond to habitat fragmentation is dependent on the range of scales relevant to each species. Each of the 10 body-size clumps determined in chapter 2 theoretically represent a group of species that respond to the same sizes of landscape objects within a similar range of scales. Grouping birds into size categories simplifies ecological analyses that explore the spatial areas and patch sizes of different birds. Once the spatial areas and patch sizes of birds are determined for each body-size clump, then researchers could predict which species (of certain sizes) will be most affected by human modifications of a landscape at a certain scale. The results of Chapter 4 allowed me to develop hypotheses about the spatial areas and patch sizes of birds in most of the 10 body-size categories (refer to tables 10 & 15). All of these results are tentative, but these results can be used as guidelines to conduct future research on the scales relevant for a variety of different bird species. For example, a researcher can use the hypotheses developed in Chapter 4 to limit the range of spatial areas and patch sizes that need to be examined for a species of a particular size. Further, the results of chapter 4 are applicable to birds that utilize other types of landscape structure, even though the analyses in chapter 4 were limited to birds that forage or nest in the tree canopy. The hypotheses developed in Chapter 4 can be used as guidelines to estimate spatial areas and patch sizes of birds that forage or nest on the ground. In this case, the landscape structure relevant to ground birds would be patches of natural open areas.

In addition, the results of chapter 4 can guide urban wildlife managers to design suburban landscapes at scales relevant to birds of different size categories. This is important because human-mediated processes that produce pattern in suburban landscapes are also scale-dependent. For example, a homeowner's backyard (small scale), a neighborhood (medium scale), and a large cluster of neighborhoods (large scale) have different processes that determine the landscape heterogeneity of each respective area. The design of a homeowner's backyard is determined by individual choice and preference; the landscape structure of a neighborhood is determined by local city ordinances, zoning laws, and the type of developer developing the neighborhood; and the landscape structure of a large cluster of neighborhoods is governed by a city's long-range comprehensive plan for large regions of a metropolitan area. The design of a suburban landscape will affect different sizes of birds depending on the pattern of remaining vegetation at different scales. Fragmentation at large scales will affect large birds whereas fragmentation at small scales will affect small birds. The results of chapter 4 (during the spring season) indicate that category 1 birds probably respond to structure within a backyard (or several backyards); category 2 birds respond to structure within portions of a neighborhood; category 3, 4, 5, 6, and 7 birds respond to structure within whole neighborhoods; and category 8 birds (and larger) respond to structure within large clusters of neighborhoods. Thus, to design a suburban landscape for a particular bird species, urban wildlife managers would have to address a specific human-mediated process that affects structure at a scale relevant to the species in question.

Finally, avian body-size clump patterns can be used to determine the hierarchical structure of different ecosystems and amount of structure available to birds at different scales. The results of Chapter 2 indicated that avian body-size clumps possibly do reflect the quantity of structure at different hierarchical levels in a landscape. For example, fewer category 2 bird species were found in a desert avian community than in temperate forest avian communities. This disparity probably reflects the decreased amount of fine texture in arid landscapes versus temperate landscapes. The comparison of Old World and New World avian communities in chapter 3 also provided further evidence that body-size clump structure reflects the unique hierarchical structure of different landscapes. Old World landscapes historically were much more fragmented than New World landscapes, and this was reflected in the avian body-size clump structure on each continent. Medium-sized bird species were much more abundant in the New World than in the Old World. This disparity is consistent with the hypothesis that fragmentation would have a greater impact on medium-sized species that either small or large species. Thus, body-size clumps can be used to estimate the amount of structure (at each hierarchical level) available to certain sizes of birds. This can be quite useful to city planners that are designing suburban landscapes in different ecoregions. For example, if one knew that a majority of the species in an avian community occurred in one body-size clump, then a development could be designed to retain the scale-dependent landscape features pertinent to these sizes of birds.

Pitfalls of using body-size clumps in landscape analyses. While avian body-size clumps greatly simplify analyses that attempt to determine what scale-dependent landscape structure birds respond to in an environment, several problems can occur in the interpretation of such analyses. First, the spatial area and resolution of an aerial photograph may not be appropriate to use when determining the spatial area and patch size that animals use to evaluate landscape structure. Aerial photos taken at high altitudes cover large spatial areas, but the resolution of an aerial photo decreases and small objects in the photo disappear along with groups of small objects fusing into one object. For large birds, the spatial area used to evaluate landscape structure can be quite large. However, the size of objects responded to by these large birds may be much smaller than the resolution of typical high-aerial photographs. Care must be given to the interpretation of landscape analyses for large birds.

Second, estimating the best patch size for birds of different body-size clumps can be quite problematic. Typically, there is a high degree of correlation between percent cover and patch sizes in a landscape; typically, landscapes with large patch sizes also have the largest amount of cover at all patch size categories. This is because large patches also contained lots of small patches, and the differences in percent cover among the sites is not that variable from one patch size category to the next. Simple regressions between bird densities and each patch size category will not reveal "peak" r^2 values. This situation is probably common for any study that compares the spatial geometry of several different landscapes. The best way to determine the best patch size of birds is to compare the densities of birds in several different sites where the percent cover of structure is similar but the geometry is totally different. For example, one site could be comprised of two large patches, another site could be comprised of 20 medium patches, and a third site could be comprised of 100 small patches; the commonality among the sites is that the percent cover is exactly the same.

Third, how a researcher measures a landscape may not reflect what certain birds are "truly" measuring. For example, certain birds may respond to clusters of scattered patches, and the best patch size for these birds is actually an aggregation of patches. This is probably true for birds that have large ambits and are able to travel between resource patches that are scattered in a landscape. Analyses would underestimate the best patch size for birds that respond to clusters of patches. On the other hand, certain birds may be responding to microhabitats within a relatively large patch. This certainly may be the case of interior forest specialists that use small patches of forest embedded in large remnants of forest (Robbins et al. 1989). In this case, analyses would overestimate the best patch size of birds that respond to microhabitat patches embedded in large patches.

Finally, the size of a bird is not always an accurate indication of the spatial area it uses to evaluate the suitability of a landscape. While object size that organisms respond to in a landscape is directly correlated to body size, the size of a spatial area (e.g., home range) is dependent on trophic status, food type, and productivity in a landscape (Haerstad and Bunnell 1979, Holling 1992b). For example, raptors have much larger home ranges than insectivorous or omnivorous birds of similar sizes. The spatial areas determined in chapter 4 are specific to insectivorous and omnivorous birds of the temperate forest biome. Thus, the spatial areas determined in chapter 4 probably do not apply to raptors. One also should not use the estimated spatial areas in Chapter 4 for avian communities in drastically different ecosystems (e.g., deserts). However, the patch sizes determined in chapter 4 apply to all species in a variety of environments.

APPENDIX A
AVIFAUNA OF VARIOUS ECOREGIONS OF NORTH AMERICA

Species and body masses of adult landbirds that breed in various ecoregions of North America (Seat = Seattle, WA; Vanc = Vancouver, B.C.; Amh = Amherst, MA; Black = Blacksburg, VA; Chic = Chicago, IL; Aus = Austin, TX; and Tuc = Tucson, AZ).

Common name	Scientific name	Body Mass (g)	Seat	Vanc	Amh	Black	Chic	Aus	Tuc
Costa's Hummingbird	*Calypta costae*	3.10	.	.	.	.	.	.	x
Ruby-throated Hummingbird	*Archilochus colubris*	3.15	.	.	x	x	x	x	.
Rufous Hummingbird	*Selasphorus rufus*	3.25	x	x	.	.	.	.	.
Black-chinned Hummingbird	*Archilochus alaxendri*	3.25	.	.	.	.	.	x	x
Anna's Hummingbird	*Calypte anna*	4.25	x	x	.	.	.	.	x
Black-tailed Gnatcatcher	*Polioptile malanura*	5.00	.	.	.	.	.	.	x
Bushtit	*Psaltriparus minimus*	5.30	x	x	.	.	.	.	.
Blue-gray Gnatcatcher	*Polioptila caarulaa*	6.00	.	.	x	x	x	x	.
Golden-crowned Kinglet	*Regulus satrapa*	6.20	x	x	x	.	.	.	.
Lucy's Warbler	*Varmivora luciaa*	6.60	.	.	.	.	.	.	x
Verdin	*Aunparus flavicaps*	6.80	.	.	.	.	.	.	x
Wilson's Warbler	*Wilsonia pusilla*	6.90	x	x	.	.	.	.	.
Northern Beardless-Tryrannulet	*Camptostoma imberbe*	7.40	.	.	.	.	.	.	x
Prairie Warbler	*Dendroica discolor*	7.65	.	.	x	x	.	.	.
American Redstart	*Stetophaga ruticilla*	8.30	.	.	x	.	x	.	.
Black-throated Gray Warbler	*Dendroica nigrescens*	8.35	x	x	.	.	.	.	.
Brown Creeper	*Certhia amancana*	8.40	x	x	x	.	.	.	.
Blue-winged Warbler	*Vermivora pinus*	8.40	.	.	x	.	x	.	.
Brown Creeper	*Carthia amancana*	8.40	.	.	.	.	.	.	.
Blue-winged Warbler	*Vermivora pinus*	8.40	.	.	.	.	.	.	.
Bells Vireo	*Virao ballii*	8.50	.	.	.	.	.	x	.
Black-capped Vireo	*Virao atricapillus*	8.50	.	.	.	.	.	x	.
Bells Vireo	*Virao bellii*	8.50	.	.	.	.	.	.	x
Northern Parula	*Parula amancana*	8.60	.	.	.	x	.	x	.
Nashville Warbler	*Vermivora ruficapilla*	8.75	.	.	x	.	.	.	.
Golden-winged Warbler	*Varmivora chrysoptara*	8.80	.	.	x	.	.	.	.
Black-throated Green Warbler	*Dendroica virens*	8.80	.	.	x	.	.	.	.
Golden-winged Warbler	*Varmivora chrysoptara*	8.80	.	.	.	.	.	.	.
Townsend's Warbler	*Dandroica townsandi*	8.85	x	x	.	.	.	.	.
Winter Wren	*Troglodytas troglodytes*	8.90	x	x	x	.	.	.	.
Orange-crowned Warbler	*Varmivora calate*	9.00	x	x	.	.	.	.	.
Sedge Wren	*Cistothorus platensis*	9.00	.	.	.	.	x	.	.
Cerulean Warbler	*Dendroica cerulaa*	9.35	.	.	.	x	x	.	.
Yellow Warbler	*Dendroica patechia*	9.50	x	x	x	x	x	.	x
Lesser Goldfinch	*Carduelis psaltria*	9.50	.	.	.	.	.	x	x
Chestnut-sided Warbler	*Dandroica pensylvanica*	9.60	.	.	x	.	.	.	.
Chestnut-backed Chickadee	*Parus rufescens*	9.70	x	x	.	.	.	.	.
Red-breasted Nuthatch	*Sitta canadensis*	9.80	x	x	x	.	.	.	.
Bewick's Wren	*Thryomanas bawickii*	9.90	x	x	.	.	.	x	x
Common Yellowthroat	*Geothlypis trichas*	10.10	x	.	.	.	.	.	.
Hammond's Flycatcher	*Empidonax hammondii*	10.10	x	x	.	.	.	.	.
Common Yellowthroat	*Geothlypis triches*	10.10	.	x	x	.	x	x	x
Black-throated Blue Warbler	*Dendroica caeruiescens*	10.15	.	.	x	.	.	.	.
Carolina Chickadee	*Parus carolinansis*	10.15	.	.	.	x	.	x	.
Golden-cheeked Warbler	*Dandroica chrysoparia*	10.20	.	.	.	.	.	x	.
Least Flycatcher	*Empidonax minimus*	10.30	.	.	x	.	x	.	.
MacGillivray's Warbler	*Oporornis tolmiai*	10.40	x	x	.	.	.	.	.
Canada Warbler	*Wilsonia canadensis*	10.40	.	.	x	x	.	.	.
Hooded Warbler	*Wilsonia citrina*	10.45	.	.	.	.	x	.	.
Canyon Wren	*Catharpes maxicanus*	10.60	.	.	.	.	.	.	x
Black-capped Chickadee	*Parus atricapillus*	10.80	x	x	x	.	x	.	.
Black-and-white Warbler	*Mniotilta varia*	10.80	.	.	x	x	x	x	.

Common name	Scientific name	Body Mass (g)	Seat	Vanc	Amh	Black	Chic	Aus	Tuc
Western Flycatcher	*Empidonax difficilis*	10.90	x	x	.	.	.	.	.
House Wren	*Troglodytes aedon*	10.90	x	x	x	x	x	.	.
Marsh Wren	*Cistothorus palustris*	11.25	x	x	.	.	.	.	.
White-eyed Vireo	*Vireo griseus*	11.40	.	.	.	x	.	x	.
Hutton's Vireo	*Vireo huttoni*	11.60	x	x	.	.	.	.	.
Varied Bunting	*Passerina versicolor*	11.80	.	.	.	.	.	.	x
Pine Warbler	*Dendroica pinus*	11.90	.	.	x	x	.	.	.
Warbling Vireo	*Vireo gilvus*	12.00	x	x	x	x	x	.	.
Chipping Sparrow	*Spizella passerina*	12.30	x	.	x	x	x	x	.
Field Sparrow	*Spizella pusilla*	12.50	.	.	x	x	x	x	.
Mourning Warbler	*Oporornis philadelphia*	12.50	.	.	.	.	x	.	.
Yellow-rumped Warbler	*Dendroica coronata*	12.55	x	x	.	.	.	.	.
Western Wood-Pewee	*Contopus sordidulus*	12.80	x	x	.	.	.	.	.
American Goldfinch	*Carduelis tristis*	12.90	x	x	x	x	x	.	.
Acadian Flycatcher	*Empidonax virescens*	12.90	.	.	.	x	x	x	.
Worm-eating Warbler	*Helmitheros vermivorus*	13.00	.	.	.	x	.	.	.
Henslow's Sparrow	*Ammodramus henslowii*	13.10	.	.	.	x	x	.	.
Willow Flycatcher	*Empidonax traillii*	13.40	x	x	x	x	x	.	.
Alder Flycatcher	*Empidonax alnorum*	13.50	.	.	x	.	.	.	.
Black-throated Sparrow	*Amphispiza bilineata*	13.50	.	.	.	.	.		x
Kentucky Warbler	*Oporornis formosus*	14.00	.	.		.	x	x	.
Eastern Wood-Pewee	*Contopus virens*	14.10	.	.	x	x	x	x	.
Violet-green Swallow	*Tachycineta thalassina*	14.15	x	x	.	.	.	.	.
Vermilion Flycatcher	*Pyrocephalus rubinus*	14.40	.	.	.	.	.	.	x
Indigo Bunting	*Passerina cyanea*	14.50	.	.	x	x	x	x	x
Pine Siskin	*Carduelis pinus*	14.60	x	x	.	.	.	.	.
Bank Swallow	*Riparia riparia*	14.60	.	.	x	.	x	.	.
Painted Bunting	*Passerina ciris*	15.55	.	.	.	.	.	x	.
Northern Rough-winged Swallow	*Stelgidopteryx serripennis*	15.90	x	x	x	x	x	.	x
Prothonotary Warbler	*Protonotaria citrea*	16.20	.	.	.	.	x	.	.
Rock Wren	*Salpinctes obsoletus*	16.50	.	.	.	.	.	.	x
Solitary Vireo	*Vireo solitarius*	16.60	x	x	x	x	.	.	.
Red-eyed Vireo	*Vireo olivaceus*	16.70	x	x	x	x	x	x	.
Swamp Sparrow	*Melospiza georgiana*	17.00	.	.	x	.	x	.	.
Grasshopper Sparrow	*Ammodramus savannarum*	17.00	.	.	.	x	x	x	.
Vaux's Swift	*Chaetura vauxi*	17.10	x	x	.	.	.	.	.
Northern Waterthrush	*Seiurus noveboracensis*	17.80	.	.	x	.	.	.	.
Yellow-throated Vireo	*Vireo flavifrons*	18.00	.	.	x	x	x	x	.
Barn Swallow	*Hirundo rustica*	18.60	x	x	x	x	x	x	x
Black Phoebe	*Sayornis nigricans*	18.65	.	.	.	.	.	.	x
Rufous-crowned Sparrow	*Aimophila ruficeps*	18.70	.	.	.	.	.	x	.
Cassin's Sparrow	*Aimophila cassinii*	18.90	.	.	.	.	.	x	.
Ovenbird	*Seiurus aurocapillus*	19.40	.	.	x	x	x	.	.
Dark-eyed Junco	*Junco hyemalis hyemalis*	19.60	x	x	x	.	.	.	.
Orchard Oriole	*Icterus spurius*	19.60	.	.	x	x	x	x	.
Eastern Phoebe	*Sayornis phoebe*	19.80	.	.	x	x	x	x	.
Savannah Sparrow	*Passerculus sandwichensis*	20.05	x	x	x	.	x	.	.
Tree Swallow	*Tachycineta bicolor*	20.10	x	x	x	.	x	.	.
Louisiana Waterthrush	*Seiurus motacilla*	20.30	.	.	.	.	x	.	.
Song Sparrow	*Melospiza melodia*	20.75	x	x	x	x	x	.	x
Carolina Wren	*Thryothorus ludovicianus*	21.00	.	.	.	x	x	x	.
White-breasted Nuthatch	*Sitta carolinensis*	21.10	.	.	x	x	x	x	x
Say's Phoebe	*Sayornis saya*	21.20	.	.	.	.	.	.	x
House Finch	*Carpodacus mexicanus*	21.40	x	x	x	x	x	x	x
Cliff Swallow	*Hirundo pyrrhonota*	21.60	x	x	x	.	x	.	x
Tufted Titmouse	*Parus bicolor*	21.60	.	.	x	x	x	x	.
Chimney Swift	*Chaetura pelagica*	23.60	.	.	x	x	x	x	.
Phainopepla	*Phainopepla nitens*	24.00	.	.	.	.	.	.	x

Common name	Scientific name	Body Mass (g)	Seat	Vanc	Amh	Black	Chic	Aus	Tuc
Hooded Oriole	*Icterus cucullatus*	24.30	.	.	.	.	.	.	x
Purple Finch	*Carpodacus purpureus*	24.90	x	x	x	.	.	.	.
White-crowned Sparrow (*Seattle subspecies*)	*Zonotrichia leucophrys pugetensis*	25.30	.	x	.	.	.	.	.
Yellow-breasted Chat	*Icteria virens*	25.30	.	.	x	x	x	x	x
Vesper Sparrow	*Pooecetes gramineus*	25.70	x	.	x	.	x	.	.
White-throated Sparrow	*Zonotrichia albicollis*	25.90	.	.	x	.	.	.	.
Dickcissel	*Spiza americana*	26.95	.	.	.	.	x	x	.
Downy Woodpecker	*Picoides pubescens*	27.00	x	x	x	x	x	x	.
Ash-throated Flycatcher	*Myiarchus cinerascens*	27.20	.	.	.	.	.	x	x
Western Bluebird	*Sialia mexicana*	28.05	x	.	.	.	.	.	.
Western Tanager	*Piranga ludoviciana*	28.10	x	x	.	.	.	.	.
Blue Grosbeak	*Guiraca caerulea*	28.40	.	.	.	x	.	x	x
Scarlet Tanager	*Piranga olivacea*	28.60	.	.	x	x	x	.	.
Lark Sparrow	*Chondestes grammacus*	28.97	.	.	.	.	x	x	.
White-crowned Sparrow (*Vancouver subspecies*)	*Zonotrichia leucophrys leucophrys*	29.40	x	.	.	.	.	.	.
Summer Tanager	*Piranga rubra*	29.80	.	.	.	x	.	x	x
Common Ground-Dove	*Columbina passerina*	30.10	.	.	.	.	.	.	x
Ladder-backed Woodpecker	*Picoides scalaris*	30.30	.	.	.	.	.	x	x
Swainson's Thrush	*Catharus ustulatus*	30.80	x	x	.	.	.	.	.
Hermit Thrush	*Catharus guttatus*	31.00	.	.	x	.	.	.	.
Veery	*Catharus fuscescens*	31.20	.	.	x	.	x	.	.
Horned Lark	*Eremophila alpestris*	31.35	.	x	x	x	x	x	x
Eastern Bluebird	*Sialia sialis*	31.60	.	.	x	x	x	x	.
Cedar Waxwing	*Bombycilla cedrorum*	31.85	x	x	x	x	x	.	.
Olive-sided Flycatcher	*Contopus borealis*	32.10	x	.	.	.	.	.	.
White-throated Swift	*Aeronautes saxatalis*	32.10	.	.	.	.	.	.	x
Great Crested Flycatcher	*Myiarchus crinitus*	33.50	.	.	x	x	x	x	.
Northern Oriole	*Icterus galbula*	33.75	x	x	x	x	x	x	x
Townsend's Solitaire	*Myadestes townsendi*	34.00	x	.	.	.	.	.	.
Pyrrhuloxia	*Cardinalis sinuatus*	35.50	.	.	.	.	.	.	x
Red Crossbill	*Loxia curvirostra*	36.50	x	x	.	.	.	.	.
Grey Catbird	*Dumetella carolinensis*	36.90	.	.	x	x	x	.	.
Scott's Oriole	*Icterus pensorum*	37.40	.	.	.	.	.	.	x
Cactus Wren	*Campylorhynchus brunneicapillus*	38.90	.	.	.	.	.	.	x
Eastern Kingbird	*Tyrannus tyrannus*	39.50	.	.	x	x	x	x	.
Western Kingbird	*Tyrannus verticalis*	39.60	.	.	.	.	.	x	x
Tropical Kingbird	*Tyrannus melancholicus*	39.80	.	.	.	.	.	.	x
Rufous-sided Towhee	*Pipilo erythrophthalmus*	40.50	x	x	x	x	x	.	x
Elf Owl	*Micrathene whitneyi*	41.00	.	.	.	.	.	.	x
Bobolink	*Dolichonyx oryzivorus*	42.05	.	.	x	.	x	.	.
Scissor-tailed Flycatcher	*Tyrannus forficatus*	43.20	.	.	.	.	.	x	.
Brown-crested Flycatcher	*Myiarchus tyrannulus*	43.80	.	.	.	.	.	.	x
Brown-headed Cowbird	*Molothrus ater*	43.90	x	x	x	x	x	x	x
Canyon Towhee	*Pipilo fuscus mesoleucus*	44.40	.	.	.	.	.	.	x
Black-headed Grosbeak	*Pheucticus melanocephalus*	44.50	x	x	.	.	.	.	.
Northern Cardinal	*Cardinalis cardinalis*	44.65	.	.	x	x	x	x	x
Rose-breasted Grosbeak	*Pheucticus ludovicianus*	45.60	.	.	x	x	x	.	.
Cassin's Kingbird	*Tyrannus vociferans*	45.60	.	.	.	.	.	.	x
Abert's Towhee	*Pipilo aberti*	45.95	.	.	.	.	.	.	x
Wood Thrush	*Hylocichla mustelina*	47.40	.	.	x	x	x	.	.
Loggerhead Shrike	*Lanius ludovicianus*	47.40	.	.	.	x	x	x	x
Inca Dove	*Columbina inca*	47.50	.	.	.	.	.	x	x
Northern Mockingbird	*Mimus polyglottos*	48.50	.	.	x	x	.	x	x
Red-breasted Sapsucker	*Sphyrapicus ruber daggetti*	48.90	x	x	.	.	.	.	.
Purple Martin	*Progne subis*	49.40	x	x	.	x	x	x	x
Lesser Nighthawk	*Chordeiles acutipennis*	49.90	.	.	.	.	.	.	x

Common name	Scientific name	Body Mass (g)	Seat	Vanc	Amh	Black	Chic	Aus	Tuc
Yellow-bellied Sapsucker	*Sphyrapicus verius verius*	50.30	.	.	x	.	.	.	.
Black-billed Cuckoo	*Coccyzus erythropthelmus*	51.10	.	.	x	x	x	.	.
Common Poorwill	*Pheleenoptilus nuttellii*	51.60	.	.	.	.	.	x	x
Red-winged Blackbird	*Agelaius phoeniceus*	52.55	x	x	x	.	x	x	x
Whip-poor-will	*Capnmulgus vociferus*	52.85	.	.	x	x	x	.	.
American Dipper	*Cinclus mexicanus*	57.80	x	x	.	.	.	.	.
Evening Grosbeak	*Coccothraustes vespertinus*	59.40	.	x	.	.	.	.	.
Red-bellied Woodpecker	*Melanerpes carolinus*	61.70	.	.	x	x	x	x	.
Common Nighthawk	*Chordeiles minor*	62.00	x	x	x	x	x	x	.
Bronzed Cowbird	*Molothrus eeneus*	62.05	.	.	.	.	.	.	x
Bendire's Thrasher	*Toxostome bendirei*	62.20	.	.	.	.	.	.	x
Brewer's Blackbird	*Euphagus cyanocephalus*	62.65	x	x	.	.	x	.	.
Crissel Thrasher	*Toxostoma crissele*	62.70	.	.	.	.	.	.	x
Yellow-billed Cuckoo	*Coccyzus emericanus*	64.00	.	.	x	x	x	x	x
Yellow-headed Blackbird	*Xanthocephalus xanthocephelus*	64.57	.	.	.	.	x	.	.
Gila Woodpecker	*Melenerpes uropygielis*	64.85	.	.	.	.	.	.	x
Hairy Woodpecker	*Picoides villosus*	86.25	x	x	x	x	x	.	.
Northern Pygmy-Owl	*Glaucidium gnoma*	67.45	x	x	.	.	.	.	.
Brown Thrasher	*Toxostome rufum*	68.80	.	.	x	x	x	.	.
Gray Jay	*Pensoreus canedensis*	71.10	x	.	.	.	.	.	.
Red-headed Woodpecker	*Melenerpes erythrocephelus*	71.60	.	.	.	x	x	x	.
American Robin	*Turdus migretorius*	77.30	x	x	x	x	x	x	.
Vened Thrush	*Ixoreus neevius*	78.40	x	x	.	.	.	.	.
Curved-billed Thrasher	*Toxostoma curvirostre*	79.40	.	.	.	.	.	.	x
Golden-fronted Woodpecker	*Melenerpes eurifrons*	80.90	.	.	.	.	.	x	.
Northern Saw-whet Owl	*Aegolius ecadicus*	82.85	x	x	x	.	.	.	.
Scrub Jay	*Aphelocoma coerulascens*	86.40	.	.	.	.	.	x	.
Blue Jay	*Cyenocitta cristeta*	86.80	.	.	x	x	x	x	.
Eastern Meadowlark	*Stumella magna*	89.00	.	.	x	x	x	x	x
Killdeer	*Cheradnus vociferus*	96.55	x	x	x	x	x	x	x
Western Meadowlark	*Sturnella neglecte*	97.70	x	x	.	.	x	.	x
Steller's Jay	*Cyanocitte stelleri*	106.00	x	x	.	.	.	.	.
Common Grackle	*Quiscalus quiscula*	113.50	.	.	x	x	x	x	.
American Kestrel	*Felco sparverius*	115.50	x	x	x	x	x	x	x
Lewis' Woodpecker	*Melanerpes lewis*	116.00	.	x	.	.	.	.	.
Mourning Dove	*Zenaida macroura*	119.00	x	x	x	x	x	x	x
Chuck-will's-widow	*Caprimulgus carolinensis*	120.00	.	.	.	.	.	x	.
Common Snipe	*Gallinego gallinego*	122.00	x	x	.	.	x	.	.
Northern Flicker	*Colaptes euratus*	132.00	x	x	x	x	x	x	x
Sharp-shinned Hawk	*Accipiter stnetus*	138.50	x	x	x	.	x	.	.
Great-tailed Grackle	*Quiscalus mexicanus*	149.00	.	.	.	.	.	x	x
White-winged Dove	*Zenaida asiatica*	153.00	.	.	.	.	.	.	x
Burrowing Owl	*Athene cuniculerie*	155.00	.	.	.	.	.	x	x
Gembel's Quail	*Callipepla gembelii*	166.00	.		.	.	.	.	x
Western Screech-Owl	*Otus kennicottii kennicottii*	169.00	x	x	.	.	.	.	x
Upland Sandpiper	*Bertremie longicauda*	169.50	.	.	x	.	x	.	.
California Quail	*Callipepla celifornice*	173.00	x	.	.	.	.	.	.
Northern Bobwhite	*Colinus virginianus*	178.00	.	.	.	x	.	x	.
Eastern Screech-Owl	*Otus esio naevius*	180.50	.	.	x	x	x	x	.
Scaled Quail	*Callipepla squamata*	184.00	.	.	.	.	.	.	x
Merlin	*Falco columbarius*	185.50	x	.	.	.	.	.	.
American Woodcock	*Scolopax minor*	197.50	.	.	x	x	x	.	.
Long-eared Owl	*Asio otus*	262.00	.	.	.	x	x	.	x
Pileated Woodpecker	*Dryocopus pileatus*	287.00	x	x	x	x	x	.	.

Appendix A (cont.)

Common name	Sciantific name	Body Mass (g)	Seat	Vanc	Amh	Black	Chic	Aus	Tuc
Band-tailed Pigeon	*Columba fasciata fasciata*	342.50	x	x	.	.	.	.	.
Short-eared Owl	*Asio flammeus*	346.50	x	x	.	.	x	.	.
Greater Roadrunnar	*Geococcyx callfornianus*	376.00	.	.	.	.	.	x	x
Gray Partridge	*Perdix pardix*	389.50	.	.	.	.	x	.	.
Northwestem Crow	*Corvus caurinus*	391.50	.	x	.	.	.	.	.
Cooper's Hawk	*Accipiter cooparii*	439.00	x	x	x	x	x	.	x
Northem Harrier	*Circus cyaneus*	440.50	x	x	.	.	x	.	.
Amarican Crow	*spp*	448.00	x	.	x	x	x	x	.
Broad-winged Hawk	*Butao platypterus*	455.00	.	.	x	x	x	.	.
Common Bam-Owl	*Tyto elba*	466.00	x	x	.	x	x	x	x
Gray Hawk	*Butao nitidis*	526.50	.	.	.	.	.	.	x
Chihuahuan Raven	*Corvus cryptolaucus*	534.00	.	.	.	.	.	.	x
Red-shouldared Hawk	*Buteo linaatus*	559.00	.	.	.	x	x	x	.
Ruffed Grousa	*Bonasa umbellus*	576.50	x	x	x	x	x	.	.
Spotted Owl	*Strix occidantalis*	609.50	x	x	.	.	.	.	.
Prairie Falcon	*Falco mexicanus*	648.50	.	.	.	.	.	.	x
Barred Owl	*Strix varia*	716.50	x	x	x	x	x	x	x
Zone-tailed Hawk	*Buteo albonotatus*	757.00	.	.	.	.	.	.	x
Peregrina Falcon	*Falco peragnnus*	781.50	x	x	.	.	.	.	x
Harris' Hawk	*Parabuteo unicinctus*	886.00	.	.	.	.	.	.	x
Crasted Caracara	*Polyborus plancus*	893.50	.	.	.	.	.	x	.
Common Black-Hawk	*Buteogallus anthracinus*	996.00	.	.	.	.	.	.	x
Glaucous-winged Gull	*Larus glaucescens*	1010.00	x	x	.	.	.	.	.
Northam Goshawk	*Accipiter gantilis*	1024.50	x	x	x	.	.	.	.
Blue Grouse	*Dendragapus obscurus*	1039.50	x	x	.	.	.	.	.
Red-tailed Hawk	*Buteo jamaicensis*	1126.00	x	x	x	x	x	x	x
Common Raven	*Corvus corax*	1199.00	x	x	.	.	.	.	x
Turkey Vultura	*Cathartes eura*	1467.00	x	x	x	x	x	x	x
Great Homed Owl	*Bubo virginianus virginianus*	1543.50	x	x	x	x	x	x	x
Bleck Vulture	*Coragyps etratus*	2080.50	.	.	.	x	.	x	.
Golden Eagle	*Aquila chrysaetos*	4308.00	.	.	.	.	.	.	x
Bald Eagle	*Haliaeetus leucocephalus*	4683.50	x	x	.	.	x	.	.
Wild Turkey	*Maleagris gallopavo*	5811.00	.	.	x	x	.	x	.

APPENDIX B
NEW WORLD AND OLD WORLD AVIFAUNA OF THE TEMPERATE BIOME

Species and body masses of adult landbirds that breed in the temperate biome of eastern North America and Europe.

Commmon Name	Scientific Name	Body Mass (g)	New World	Old World
Ruby-throated Hummingbird	Archilochus colubris	3.15	x	.
Firecrest	Regalus ignicepillus	5.60	.	x
Goldcrest	Regulus regulus	5.70	.	x
Blue-gray Gnatcatcher	Polioptila caerulee	6.00	x	.
Golden-crowned Kinglet	Regulus setrape	6.20	x	.
Ruby-crowned Kinglet	Regulus calendula	6.65	x	.
Wilson's Warbler	Wilsonie pusilla	6.90	x	.
Fan-tailed Warbler	Cisticole juncidis	7.05	.	x
Bonelli's Warbler	Phylloscopus bonelli	7.20	.	x
Chiffchaff	Phylloscopus collybita	7.50	.	x
Prairie Warbler	Dendroica discolor	7.65	x	.
Long-tailed Tit	Aegithalos caudetus	8.20	.	x
Wood Warbler	Phylloscopus sibilatri	8.20	.	x
American Redstart	Stetophega ruticille	8.30	x	.
Brown Creeper	Certhie emericana	8.40	x	.
Blue-winged Warbler	Vermivora pinus	8.40	x	.
Short-toed treecreeper	Certhia brechydactyla	8.50	.	x
Bells Vireo	Vireo bellii	8.50	x	.
Northern Parula	Parula emericana	8.60	x	.
Magnolia Warbler	Dendroica megnolie	8.70	x	.
Nashville Warbler	Vermivora ruficapille	8.75	x	.
Black-thrt Green Warbler	Dendroica virens	8.80	x	.
Golden-winged Warbler	Vermivora chrysoptere	8.80	x	.
Winter Wren	Troglodytes troglodytes	8.90	x	x
Treecreeper	Certhia femilleris	9.00	.	x
Sedge Wren	Cistothorus platensis	9.00	x	.
Coal Tit	Parus ater	9.10	.	x
Penduline Tit	Remiz pendulinus	9.30	.	x
Cerulean Warbler	Dendroica cerulea	9.35	x	.
Yellow-throated Warbler	Dendroica dominice	9.40	x	.
Yellow Warbler	Dendroica petechie	9.50	x	.
Greenish Warbler	Phylloscopus trochilo	9.50	.	x
Willow Warbler	Phylloscopus trochilus	9.50	.	x
Chestnut-sided Warbler	Dendroice pensylvenica	9.60	x	.
Blackburnian Warbler	Dendroica fusca	9.75	x	.
Boreal Chickadee	Parus hudsonicus	9.80	x	.
Red-breasted Nuthatch	Sitte canadensis	9.80	x	.
Bewick's Wren	Thryomenes bewickii	9.90	x	.
Tennessee Warbler	Vermivora peregrine	10.00	x	.
Common Yellowthroat	Geothlypis triches	10.10	x	.
Lesser Whitethroat	Sylvia curruce	10.10	.	x
Black-throated Blue Warbler	Dendroica caerulescens	10.15	x	.
Carolina Chickadee	Parus cerolinensis	10.15	x	.
Crested Tit	Perus cristatus	10.20	.	x
Willow Tit	Parus montanus	10.20	.	x
Brown-headed Nuthatch	Sitte pusille	10.20	x	.

Commmon Name	Scientific Name	Body Mass (g)	New World	Old World
Palm Warbler	Dendroica palmarum	10.30	x	.
Least Flycatcher	Empidonax minimus	10.30	x	.
Collared Flycatcher	Ficedula albicollis	10.30	.	x
Canada Warbler	Wilsonia canadensis	10.40	x	.
Hooded Warbler	Wilsonia citrina	10.45	x	.
Marsh Tit	Parus palustris	10.60	.	x
Red-breasted Flycatcher	Ficedula parva	10.70	.	x
Black-and-white Warbler	Mniotilta varia	10.80	x	.
Black-capped Chickadee	Parus atricapillus	10.80	x	.
Dartford Warbler	Sylvia undata	10.80	.	x
House Wren	Troglodytes aedon	10.90	x	.
Cape May Warbler	Dendroica tigrina	11.00	x	.
Melodious Warbler	Hippolais polyglotta	11.00	.	x
Sedge Warbler	Acrocephalus schoenobaenus	11.20	.	x
Serin	Serinus serinus	11.20	.	x
Marsh Wren	Cistothorus palustris	11.25	x	.
White-eyed Vireo	Vireo griseus	11.40	x	.
Yellow-bellied Flycatcher	Empidonax flaviventris	11.60	x	.
Pied Flycatcher	Ficedula hypoleuca	11.60	.	x
Marsh Warbler	Acrocephalus palustris	11.90	.	x
Pine Warbler	Dendroica pinus	11.90	x	.
Citril Finch	Serinus citrinella	12.00	.	x
Warbling Vireo	Vireo gilvus	12.00	x	.
Philadelphia Vireo	Vireo philadelphicus	12.20	x	.
Mourning Warbler	Oporornis philadelphia	12.50	x	.
Bay-breasted Warbler	Dendroica castanea	12.55	x	.
Yellow-rumped Warbler	Dendroica coronata	12.55	x	.
American Goldfinch	Carduelis tristis	12.90	x	.
Acadian Flycatcher	Empidonax virescens	12.90	x	.
Redpoll	Carduelis flammea	13.00	.	x
Blackpoll Warbler	Dendroica striata	13.00	x	.
Worm-eating Warbler	Helmitheros vermivorus	13.00	x	.
Grasshopper Warbler	Locustella naevia	13.30	.	x
Blue Tit	Parus caeruleus	13.30	.	x
Willow Flycatcher	Empidonax traillii	13.40	x	.
Alder Flycatcher	Empidonax alnorum	13.50	x	.
Kirtland's Warbler	Dendroica kirtlandii	13.80	x	.
Garden Warbler	Sylvia borin	13.90	.	x
Kentucky Warbler	Oporornis formosus	14.00	x	.
Eastern Wood-Pewee	Contopus virens	14.10	x	.
Cetti's Warbler	Cettia cetti	14.25	.	x
Siskin	Carduelis spinus	14.50	.	x
House Martin	Delichon urbica	14.50	.	x
Pine Siskin	Carduelis pinus	14.60	x	.
Icterine Warbler	Hippolais icterina	14.60	.	x
Spotted Flycatcher	Muscicapa striata	14.60	.	x
Redstart	Phoenicurus phoenicurus	14.60	.	x
Sand Martin/Bank Swallow	Riparia riparia	14.60	x	x
Savi's Warbler	Locustella luscinioides	15.00	.	x
Connecticut Warbler	Oporornis agilis	15.20	x	.
Rough-winged Swallow	Stelgidopteryx ruficollis	15.20	x	.
Linnet	Carduelis cannabina	15.30	.	x
Stonechat	Saxicola torquata	15.30	.	x
Twite	Carduelis flavirostris	15.40	.	x
Blackcap	Sylvia atricapilla	15.50	.	x
Goldfinch	Carduelis carduelis	15.60	.	x
Bearded Tit	Panurus biarmicus	15.70	.	x
Swallow	Hirundo rustica	16.00	.	x

Commmon Name	Scientific Name	Body Mass (g)	New World	Old World
Prothonotary Warbler	Protonotaria citrea	16.20	x	.
Black Redstart	Phoenicurus ochruros	16.50	.	x
Whinchat	Saxicola rubetra	16.60	.	x
Wall Creeper	Tichodroma muraria	16.60	.	x
Solitary Vireo	Vireo solitarius	16.60	x	.
Red-eyed Vireo	Vireo olivaceus	16.70	x	.
Grey Wagtail	Motacilla cinerea	17.60	.	x
Blue-headed Wagtail	Motacilla flave flava	17.60	.	x
Northern Waterthrush	Seiurus noveboracensis	17.80	x	.
Black-whiskered Vireo	Vireo altiloquus	17.90	x	.
Yellow-throated Vireo	Vireo flavitrons	18.00	x	.
River Warbler	Locustella fluviatilis	18.10	.	x
Robin	Erithacus rubecula	18.20	.	x
Bluethroat	Luscinia svecica	18.20	.	x
Reed Bunting	Emberize schoeniclus	18.30	.	x
Nightingale	Luscinia megarhynchos	18.30	.	x
Meadow Pipit	Anthus pratensis	18.40	.	x
Barn Swallow	Hirundo rustica	18.60	x	.
Swainson's Warbler	Limnothlypis swainsonii	18.90	x	.
Great Tit	Parus major	19.00	.	x
Rock Bunting	Emberiza cia	19.30	.	x
Ovenbird	Seiurus aurocapillus	19.40	x	.
Orcherd Oriole	Ictarus spurius	19.60	x	.
Dark-eyad Junco	Junco hyemalis hyemalis	19.60	x	.
Dunnock	Prunella moduleris	19.70	.	x
Lesser Spotted Woodpecker	Dendrocopos minor	19.80	.	x
Eastern Phoebe	Sayomis phoebe	19.80	x	.
Tree Swallow	Tachycinata bicolor	20.10	x	.
Louisiana Watarthrush	Seiurus motacilla	20.30	x	.
White Wegtail	Motacilla alba alba	21.00	.	x
Pied Wagteil	Motacilla alba yarrallii	21.00	.	x
Carolina Wran	Thryothorus ludovicienus	21.00	x	.
Whita-breasted Nuthatch	Sitta carolinensis	21.10	x	.
House Finch	Carpodacus mexicanus	21.40	x	.
Chaffinch	Fringilla coelabs	21.40	.	x
Cliff Swallow	Hirundo pyrrhonota	21.60	x	.
Tufted Titmouse	Parus bicolor	21.60	x	.
Bullfinch	Pyrrhula pyrrhula	21.80	.	x
Trae Sperrow	Passer montanus	22.00	.	x
Nuthatch	Sitta europaea	22.00	.	x
Barred Warbler	Sylvia nisoria	22.80	.	x
Tawny Pipit	Anthus campestris	23.00	.	x
Cirl Bunting	Emberiza cirlus	23.10	.	x
Wheatear	Oenanthe oenanthe	23.15	.	x
Tree Pipit	Anthus trivialis	23.40	.	x
Rock Pipit	Anthus petrosus	23.50	.	x
Chimney Swift	Chaetura pelagica	23.60	x	.
Ortolen Bunting	Enbanza hortulena	23.80	.	x
Thrush Nightingale	Luscinia luscinia	23.80	.	x
Water Pipit	Anthus spinoletta	23.90	.	x
Scarlet Grosbeek	Cerpodacus erythrinus	24.10	.	x
Purple Finch	Carpodacus purpureus	24.90	x	.
Yellow-breasted Chat	Icteria virens	25.30	x	.
Yellowhammer	Emberiza citrinella	26.50	.	x
White-winged Crossbill	Loxia leucoptera	26.60	x	.
Woodlark	Lullula arborea	26.90	.	x

Commmon Name	Scientific Nema	Body Mass (g)	Naw World	Old World
Dickcissel	Spiza emericana	26.95	x	.
Kingfisher	Alcedo etthis	27.00	.	x
Downy Woodpecker	Picoides pubescens	27.00	x	.
Great Reed Warbler	Acrocephalus arundineceus	27.20	.	x
Housa Sperrow	Passer domasticus	27.70	.	x
Graenfinch	Cardualis chloris	27.80	.	x
Blue Grosbeak	Guirace caerulee	28.40	x	.
Scarlet Tanager	Piranga olivecea	28.60	x	.
Woodchat Shrike	Lanius senetor	29.10	.	x
Summer Teneger	Pirenge rubre	29.80	x	.
Red-becked Shrike	Lanius collurio	29.90	.	x
Common Ground-Dove	Columbina passerina	30.10	x	.
Swainson's Thrush	Catharus ustulatus	30.80	x	.
Hermit Thrush	Catharus guttatus	31.00	x	.
Vaery	Catharus fuscascens	31.20	x	.
Horned Lark	Eremophila elpastris	31.35	x	.
Eastern Bluebird	Sialia sialis	31.60	x	.
Cedar Waxwing	Bombycilla cedrorum	31.85	x	.
Olive-sided Flycetcher	Contopus borealis	32.10	x	.
Pygmy Owl	Glaucidium passarinum	32.62	.	x
Gray-cheeked Thrush	Catharus minimus	32.80	x	.
Wryneck	Jynx torquilla	33.50	.	x
Great Crested Flycatcher	Myierchus crinitus	33.50	x	.
Northern Oriola	Icterus galbule	33.75	x	.
Red Crossbill	Loxia curvirostre	36.50	x	.
Gray Catbird	Dumetelle cerolinensis	36.90	x	.
Swift	Apus apus	37.60	.	x
Skylerk	Alauda arvensis	38.95	.	x
Eastern Kingbird	Tyrennus tyrannus	39.50	x	.
Western Kingbird	Tyrennus varticalis	39.60	x	.
Crested Lark	Galeride cristata	40.45	.	x
Rufous-sided Towhee	Pipilo erythrophthalmus	40.50	x	.
Crossbill	Loxia curvirostra	40.60	.	x
Bobolink	Dolichonyx oryzivorus	42.05	x	.
Scissor-tailed Flycetchar	Tyrannus forficatus	43.20	x	.
Red-cockaded Woodpecker	Picoides borealis	43.60	x	.
Alpine Accentor	Prunelle colleris	43.70	.	x
Brown-headed Cowbird	Molothrus ater	43.90	x	.
Grey Kingbird	Tyrannus dominicensis	43.90	x	.
Northern Cerdinel	Cerdinelis cardinalis	44.65	x	.
Corn Bunting	Milieria celendra	46.00	.	x
Wood Thrush	Hylocichla mustelina	47.40	x	.
Loggerhead Shrika	Lanius ludovicianus	47.40	x	.
Northarn Mockingbird	Mimus polyglottos	48.50	x	.
Rock Thrush	Monticole sexitilis	48.50	.	x
Lesser Grey Shrike	Lanius minor	48.60	.	x
Purpla Martin	Progne subis	49.40	x	.
Yellow-ballied Sapsuckar	Sphyrapicus varius varius	50.30	x	.
Black-billed Cuckoo	Coccyzus arythropthalmus	51.10	x	.
Red-wingad Blackbird	Ageleius phoeniceus	52.55	x	.
Whip-poor-will	Caprimulgus vociferus	52.95	x	.
Parrot Crossbill	Loxia pytyopsittacus	53.00	.	x
Hewfinch	Coccothraustes coccothraustas	54.00	.	x
Bae-eater	Morops apiastar	56.60	.	x
Middla-spotted Woodpecker	Dendrocops medius	59.00	.	x
Evening Grosbeak	Coccothraustes vespertinus	59.40	x	.

Commmon Name	Scientific Name	Body Mass (g)	New World	Old World
Rusty Blackbird	Euphagus carolinus	59.75	x	.
Dipper	Cinclus cinclus	59.80	.	x
Redwing	Turdus iliacus	61.20	.	x
Hoopoe	Upupa epops	61.40	.	x
Red-bellied Woodpecker	Melanerpes carolinus	61.70	x	.
Common Nighthawk	Chordeiles minor	62.00	x	.
Brewer's Blackbird	Euphagus cyanocephalus	62.65	x	.
Mangrove Cuckoo	Coccyzus minor	63.90	x	.
Yellow-billed Cuckoo	Coccyzus americanus	64.00	x	.
Yellow-headed Blackbird	Xanthocephalus xanthocephalus	64.50	x	.
Great Grey Shrike	Lanius excubitor	65.60	.	x
Three-toed Woodpecker	Picoides tridactylus	65.65	x	x
Hairy Woodpecker	Picoides villosus	66.25	x	.
Rose-coloured Starling	Sturnus roseus	66.50	.	x
Nightjar	Caprimulgus europaeus	67.00	.	x
Song Thrush	Turdus philomelos	67.75	.	x
Brown Thrasher	Toxostoma rufum	68.80	x	.
Black-backed Woodpecker	Picoides arcticus	69.30	x	.
Gray Jay	Perisoreus canadensis	71.10	x	.
Red-headed Woodpecker	Melanerpes erythrocephalus	71.60	x	.
Syrian Woodpecker	Dendrocopos syriacus	76.25	.	x
American Robin	Turdus migratorius	77.30	x	.
Golden Oriole	Oriolus oriolus	79.00	.	x
Great Spotted Woodpecker	Dendrocopos major	81.60	.	x
Starling	Sturnus vulgaris	82.30	.	x
Northern Saw-whet Owl	Aegolius acadicus	82.85	x	.
Scrub Jay	Aphelocoma coerulescens	86.40	x	.
Blue Jay	Cyanocitta cristata	86.80	x	.
Eastern Meadowlark	Sturnella magna	89.00	x	.
Scops Owl	Otus scops	92.00	.	x
Western Meadowlark	Sturnella neglecta	97.70	x	.
Quail	Coturnix coturnix	101.50	.	x
Smooth-billed Ani	Crotophaga ani	105.00	x	.
Fieldfare	Turdus pilaris	106.00	.	x
Ring Ouzel	Turdus torquatus	109.00	.	x
Cuckoo	Cuculus Canorus	113.00	.	x
Blackbird	Turdus merula	113.00	.	x
Common Grackle	Quiscalus quiscula	113.50	x	.
Mistle Thrush	Turdus viscivorus	115.00	.	x
American Kestrel	Falco sparverius	115.50	x	.
Mourning Dove	Zenaida macroura	119.00	x	.
Chuck-will's-widow	Caprimulgus carolinensis	120.00	x	.
Northern Flicker	Colaptes auratus	132.00	x	.
Turtle Dove	Sterptopelia turtur	132.00	.	x
Tengmalm's Owl	Aegolius funereus	134.00	.	x
Grey-headed Woodpecker	Picus canus	137.00	.	x
Sharp-shinned Hawk	Accipiter striatus	138.50	x	.
Roller	Coracias garrulus	146.00	.	x
Belted Kingfisher	Ceryle alcyon	148.00	x	.
Great-tailed Grackle	Quiscalus mexicanus	149.00	x	.
Collared Dove	Streptopelia decaocto	149.00	.	x
Jay	Garrulus glandarius	161.00	.	x
Little Owl	Athene noctua	164.00	.	x
Boat-tailed Grackle	Quiscalus major	166.50	x	.
Nutcracker	Nucifraga caryocatactes	172.50	.	x
Green Woodpecker	Picus viridis	176.00	.	x

Commmon Name	Scientific Name	Body Mass (g)	New World	Old World
Magpie	Pica pica	177.50	.	x
Northern Bobwhite	Colinus virginienus	178.00	x	.
Eastern Screech-Owl	Otus esio naevius	180.50	x	.
Merlin	Falco columbarius	185.50	.	x
Kestrel	Felco tinnunculus	201.50	.	x
Chough	Pyrrhocorax graculus	223.50	.	x
Sparrowhawk	Accipiter nisus	237.50	.	x
Hobby	Felco subbuteo	240.00	.	x
Jackdaw	Corvus monedula	246.00	.	x
Long-eared Owl	Asio otus	262.00	x	x
Mississippi Kite	Ictinie mississippiensis	281.00	x	.
Fish Crow	Corvus ossifragus	285.00	x	.
Pileated Woodpecker	Dryocopus pileatus	287.00	x	.
Stock Dove	Columba oenas	291.00	.	x
Barn Owl	Tyto alba	294.00	.	x
Montagu's Harrier	Circus pygargus	315.50	.	x
Black Woodpecker	Dryocopus mertius	321.00	.	x
Short-eared Owl	Asio flammeus	346.50	x	x
Rock Dove	Columba livia	354.50	.	x
Greater Roadrunner	Geococcyx celifornienus	376.00	x	.
Snail Kite	Rostrhemus sociebilis	380.00	x	.
Grey Partridge	Perdix perdix	389.50	x	x
Rock Ptarmigan	Lagopus mutus	425.00	.	x
Hazelhen	Bonasa bonasia	429.00	.	x
Northern/Hen Harrier	Circus cyeneus	435.50	x	x
Cooper's Hawk	Accipiter cooperii	439.00	x	.
American Crow	Corvus brachyrhynchos	448.00	x	.
Broad-winged Hawk	Buteo pletypterus	455.00	x	.
Common Barn-Owl	Tyto alba	466.00	x	.
Spruce Grouse	Dendragapus canadensis	474.00	x	.
American Swallow-tailed Kite	Elanoides forficatus	475.00	x	.
Tawny Owl	Strix eluco	475.00	.	x
Red-legged Partridge	Alectoris rufe	483.00	.	x
Rook	Corvus frugilegus	488.00	.	x
Short-tailed Hawk	Buteo brachyurus	495.00	x	.
Red Grouse	Lagopus legopus scoticus	558.50	.	x
Red-shouldered Hawk	Buteo lineatus	559.00	x	.
Hooded Crow	Corvus corone cornix	570.00	.	x
Carrion Crow	Corvus corone corone	570.00	.	x
Ruffed Grouse	Bonesa umbellus	576.50	x	.
Marsh Harrier	Circus eeruginosus	627.50	.	x
Barred Owl	Strix varia	716.50	x	.
Lesser Prairie-Chicken	Tympenuchus pellidicinctus	755.50	x	.
Honey Buzzard	Pernis apivorus	758.00	.	x
Peregrine Falcon	Falco peregrinus	781.50	.	x
Ural Owl	Strix uralensis	784.50	.	x
Black Kite	Milvus migrans	827.00	.	x
Buzzard	Buteo buteo	875.00	.	x
Sharp-tailed Grouse	Tympanuchus phasienellus	885.00	x	.
Greater Prairie-Chicken	Tympanuchus cupido	885.50	x	.
Crested Ceracara	Polyborus plencus	893.50	x	.
Swainson's Hawk	Buteo swainsoni	988.50	x	.
Northern Goshawk	Accipiter gentilis	1024.50	x	x
Red Kite	Milvus milvus	1080.00	.	x
Black Grouse	Tetrao tetrix	1082.50	.	x
Red-tailed Hawk	Buteo jamaicensis	1126.00	x	.

Commmon Name	Scientific Name	Body Mass (g)	New World	Old World
Ring-necked Pheasant	Phasianus colchicus	1135.00	x	.
Pheasant	Phesianus colchicus	1135.00	.	x
Common Raven	Corvus corax	1199.00	x	.
Raven	Corvus corax	1199.00	.	x
Lesser Spotted Eagle	Aquila pomenna	1370.00	.	x
Turkey Vulture	Cethartes eure	1467.00	x	.
Osprey	Pendion heliaetus	1485.50	x	x
Great Horned Owl	Bubo virginianus virginianus	1543.50	x	.
Black Vulture	Coregyps atratus	2080.50	x	.
Spotted Eagle	Aquila clenge	2205.50	.	x
Eagle Owl	Bubo bubo	2686.00	.	x
Cepercaillie	Tetrao urogallus	2950.00	.	x
Imperial Eagle	Aquila heliaca	3395.00	.	x
Golden Eagle	Aquila chrysaetos	4195.00	.	x
Short-toed Eagle	Aquila chrysaetos	4195.00	.	x
Bald Eagle	Halieeetus leucocephelus	4683.50	x	.
Wild Turkey	Meleagris gellopavo	5811.00	x	.

APPENDIX C
NEW WORLD AND OLD WORLD AVIFAUNA OF THE BOREAL BIOME

Species and body masses of adult landbirds that breed in the boreal biome of eastern North America and Europe.

Common name	Scientific name	Body Mass (g)	New World	Old World
Ruby-throated Hummingbird	*Archilochus colubris*	3.15	x	.
Goldcrest	*Regulus ragulus*	5.70	.	x
Golden-crowned Kinglet	*Regulus setrapa*	6.20	x	.
Ruby-crowned Kinglet	*Regulus calendule*	6.65	x	.
Wilson's Warbler	*Wilsonie pusille*	6.90	x	.
Chiffcheff	*Phylloscopus collybite*	7.50	.	x
Long-tailed Tit	*Aegithelos caudatus*	8.20	.	x
Wood Warbler	*Phylloscopus sibiletri*	8.20	.	x
American Redstart	*Stetophaga ruticille*	8.30	x	.
Brown Creeper	*Certhie americana*	8.40	x	.
Northern Parule	*Perule americene*	8.60	x	.
Magnolia Warbler	*Dendroice megnolie*	8.70	x	.
Nashville Warbler	*Vermivore ruficepilla*	8.75	x	.
Black-throated Green Warbler	*Dendroice virens*	8.80	x	.
Winter Wren	*Troglodytes troglodytes*	8.90	x	x
Treecreeper	*Certhie familiaris*	9.00	.	x
Sedge Wren	*Cistothorus platensis*	9.00	x	.
Orange-crowned Warbler	*Vermivora celeta*	9.00	x	.
Coal Tit	*Perus ater*	9.10	.	x
Yellow Warbler	*Dendroica petechie*	9.50	x	.
Greenish Warbler	*Phylloscopus trochilo*	9.50	.	x
Willow Warbler	*Phylloscopus trochilus*	9.50	.	x
Chestnut-sided Warbler	*Dendroice pensylvanica*	9.60	x	.
Bleckburnian Warbler	*Dendroice fusca*	9.75	x	.
Boreal Chickadee	*Parus hudsonicus*	9.80	x	.
Red-breasted Nuthatch	*Sitta canedensis*	9.80	x	.
Tennessee Warbler	*Vermivora peregrine*	10.00	x	.
Lesser Whitethroat	*Sylvie curruca*	10.10	.	x
Crested Tit	*Parus cristetus*	10.20	.	x
Willow Tit	*Parus montanus*	10.20	.	x
Palm Warbler	*Dendroice palmarum*	10.30	x	.
Least Flycatcher	*Empidonax minimus*	10.30	x	.
House Wren	*Troglodytes eedon brunneicollis*	10.40	x	.
Canada Warbler	*Wilsonia cenedensis*	10.40	x	.
March Tit	*Perus palustris*	10.60	.	x
Red-breasted Flycatcher	*Ficedule parve*	10.70	.	x
Black-capped Chickadee	*Perus atricepillus*	10.80	x	.
House Wren	*Troglodytes eedon*	10.90	x	.
Cape May Warbler	*Dendroica tigrine*	11.00	x	.
Blyth's Reed Warbler	*Acrocephelus dumetorum*	11.20	.	x
Yellow-belled Flycatcher	*Empidonex fleviventris*	11.60	x	.
Pied Flycatcher	*Ficedule hypoleuce*	11.60	.	x
Pine Warbler	*Dendroica pinus*	11.90	x	.
Warbling Vireo	*Vireo gilvus*	12.00	x	.
Philadelphia Vireo	*Vireo philedelphicus*	12.20	x	.
Chipping Sparrow	*Spizelle passerine*	12.30	x	.

Common name	Scientific name	BodyMass (g)	New World	Old World
Siberian Tit	*Parus cinctus*	12.40	.	x
Mourning Warbler	*Oporornis philadelphia*	12.50	x	.
Bay-breasted Warbler	*Dendroica castanea*	12.55	x	.
Yellow-rumped Warbler	*Dendroica coronata*	12.55	x	.
Arctic/Hoary Redpoll	*Carduelis hornemanni*	12.70	x	x
American Goldfinch	*Carduelis tristis*	12.90	x	.
Redpoll	*Carduelis flammea*	13.00	x	x
Blue Tit	*Parus caeruleus*	13.30	.	x
Le Conte's Sparrow	*Ammodramus lecontei*	13.40	x	.
Garden Warbler	*Sylvia borin*	13.90	.	x
Eastern Wood-Pewee	*Contopus virens*	14.10	x	.
Siskin	*Carduelis spinus*	14.50	.	x
House Martin	*Delichon urbica*	14.50	.	x
Indigo Bunting	*Passerina cyanea*	14.50	x	.
Whitethroat	*Sylvia communis*	14.50	.	x
Pine Siskin	*Carduelis pinus*	14.60	x	.
Icterine Warbler	*Hippolais icterina*	14.60	.	x
Spotted Flycatcher	*Muscicapa striata*	14.60	.	x
Redstart	*Phoenicurus phoenicurus*	14.60	.	x
Bank Swallow	*Riparia riparia*	14.60	x	.
Connecticut Warbler	*Oporornis agilis*	15.20	x	.
Linnet	*Carduelis cannabina*	15.30	.	x
Blackcap	*Sylvia atricapilla*	15.50	.	x
Goldfinch	*Carduelis carduelis*	15.60	.	x
Barn Swallow	*Hirundo rustica*	16.00	x	x
Whinchat	*Saxicola rubetra*	16.60	.	x
Solitary Vireo	*Vireo solitarius*	16.60	x	.
Red-eyed Vireo	*Vireo olivaceus*	16.70	x	.
Lincoln's Sparrow	*Melospiza lincolnii*	17.40	x	.
Red-eyed Vireo	*Vireo olivaceus flavoviridis*	17.90	x	.
Robin	*Erithacus rubecula*	18.20	.	x
Reed Bunting	*Emberiza schoeniclus*	18.30	.	x
Meadow Pipit	*Anthus pratensis*	18.40	.	x
Great Tit	*Parus major*	19.00	.	x
Northern Junco	*Junco hyemalis (oreganus)*	19.30	x	.
Ovenbird	*Seiurus aurocapillus*	19.40	x	.
Dunnock	*Prunella modularis*	19.70	.	x
Lesser Spotted Woodpecker	*Dendrocopos minor*	19.80	.	x
Eastern Phoebe	*Sayornis phoebe*	19.80	x	.
Savannah Sparrow	*Passerculus sandwichensis*	20.05	x	.
Tree Swallow	*Tachycineta bicolor*	20.10	x	.
Citrine Wagtail	*Motacilla citreola*	20.30	.	x
Song Sparrow	*Melospiza melodia*	20.75	x	.
Least Sandpiper	*Calidris minutilla*	20.90	x	.
White-breasted Nuthatch	*Sitta carolinensis*	21.10	x	.
Chaffinch	*Fringilla coelebs*	21.40	.	x
Cliff Swallow	*Hirundo pyrrhonota*	21.60	x	.
Yellow-breasted Bunting	*Emberiza aureola*	21.70	.	x
Bullfinch	*Pyrrhula pyrrhula*	21.80	.	x
Tree Sparrow	*Passer montanus*	22.00	.	x
Nuthatch	*Sitta europaea*	22.00	.	x
Barred Warbler	*Sylvia nisoria*	22.80	.	x
Tree Pipit	*Anthus trivialis*	23.40	.	x
Chimney Swift	*Chaetura pelagica*	23.60	x	.
Ortolan Bunting	*Emberiza hortulana*	23.80	.	x
Brambling	*Fringilla montifringilla*	24.00	.	x
Scarlet Grosbeak	*Carpodacus erythrinus*	24.10	.	x

Common name	Scientific name	Body Mass (g)	New World	Old World
Purple Finch	*Carpodacus purpureus*	24.90	x	.
Sprague's Pipit	*Anthus spragueii*	25.30	x	.
Vesper Sparrow	*Pooecetes gramineus*	25.70	x	.
White-throated Sparrow	*Zonotrichia albicollis*	25.90	x	.
Smith's Longspur	*Calcarius pictus*	26.40	x	.
Yellowhammer	*Emberiza citrinella*	26.50	.	x
White-winged Crossbill	*Loxia leucoptera*	26.60	x	.
Woodlark	*Lullula arborea*	26.90	.	x
Downy Woodpecker	*Picoides pubescens*	27.00	x	.
Lapland Longspur	*Calcarius lapponicus*	27.30	x	x
House Sparrow	*Passer domesticus*	27.70	.	x
Greenfinch	*Carduelis chloris*	27.80	.	x
Red-backed Shrike	*Lanius collurio*	29.90	.	x
Swainson's Thrush	*Catharus ustulatus*	30.80	x	.
Hermit Thrush	*Catharus guttatus*	31.00	x	.
Veery	*Catharus fuscescens*	31.20	x	.
Horned Lark	*Eremophila alpestris*	31.35	x	.
Eastern Bluebird	*Sialia sialis*	31.60	x	.
Cedar Waxwing	*Bombycilla cedrorum*	31.85	x	.
Olive-sided Flycatcher	*Contopus borealis*	32.10	x	.
Fox Sparrow	*Passerella iliaca*	32.30	x	.
Pygmy Owl	*Glaucidium passerinum*	32.62	.	x
Wryneck	*Jynx torquilla*	33.50	.	x
Great Crested Flycatcher	*Myiarchus crinitus*	33.50	x	.
Northern Oriole	*Icterus galbula*	33.75	x	.
Harris' Sparrow	*Zonotrichia querula*	36.25	x	.
Red Crossbill	*Loxia curvirostra*	36.50	x	.
Grey Catbird	*Dumetella carolinensis*	36.90	x	.
Swift	*Apus apus*	37.60	.	x
Skylark	*Alauda arvensis*	38.95	.	x
Eastern Kingbird	*Tyrannus tyrannus*	39.50	x	.
Western Kingbird	*Tyrannus verticalis*	39.60	x	.
Crossbill	*Loxia curvirostra*	40.60	.	x
Brown-headed Cowbird	*Molothrus ater*	43.90	x	.
Rose-breasted Grosbeak	*Pheucticus ludovicianus*	45.60	x	.
Semipalmated Plover	*Charadrius semipalmatus*	46.75	x	.
Yellow-bellied Sapsucker	*Sphyrapicus varius varius*	50.30	x	.
Black-billed Cuckoo	*Coccyzus erythropthalmus*	51.10	x	.
Yellow Rail	*Coturnicops noveboracensis*	51.60	x	.
Whip-poor-will	*Caprimulgus vociferus*	52.80	x	.
Parrot Crossbill	*Loxia pytyopsittacus*	53.00	.	x
Waxwing	*Bombycilla garrulus*	56.40	.	x
Pine Grosbeak	*Pinicola enucleator*	56.40	x	x
Evening Grosbeak	*Coccothraustes vespertinus*	59.40	x	.
Redwing	*Turdus iliacus*	61.20	.	x
Common Nighthawk	*Chordeiles minor*	62.00	x	.
Brewer's Blackbird	*Euphagus cyanocephalus*	62.65	x	.
Yellow-headed Blackbird	*Xanthocephalus xanthocephalus*	64.50	x	.
Great Grey Shrike	*Lanius excubitor*	65.60	.	x
Three-toed Woodpecker	*Picoides tridactylus*	65.65	x	x
Hairy Woodpecker	*Picoides villosus*	66.25	x	.
Nightjar	*Caprimulgus europaeus*	67.00	.	x
Song Thrush	*Turdus philomelos*	67.75	.	x
Brown Thrasher	*Toxostoma rufum*	68.80	x	.
Black-backed Woodpecker	*Picoides arcticus*	69.30	x	.
Gray Jay	*Perisoreus canadensis*	71.10	x	.

Common name	Scientific name	Body Mass (g)	New World	Old World
Red-headed Woodpecker	*Melenerpes erythrocephelus*	71.60	x	.
American Robin	*Turdus migretorius*	77.30	x	.
Great Spotted Woodpecker	*Dendrocopos major*	81.60	.	x
Starling	*Stumus vulgens*	82.30	.	x
Northern Saw-whet Owl	*Aegolius acadicus*	82.85	x	.
Siberian Jay	*Perisoreus infaustus*	84.40	.	x
Blue Jay	*Cyenocitte cnsteta*	86.80	x	.
Eastern Meadowlark	*Stumella magne*	89.00	x	.
Western Meadowlark	*Stumella neglecta*	97.70	x	.
Fieldfare	*Turdus pilaris*	106.00	.	x
Dotterel	*Cheradrius morinellus*	108.50	.	x
Ring Ouzel	*Turdus torquatus*	109.00	.	x
Northern Flicker	*Coleptes auratus meemsi*	111.00	x	.
Cuckoo	*Cuculus Canorus*	113.00	.	x
Blackbird	*Turdus merula*	113.00	.	x
Common Grackle	*Quiscalus quiscule*	113.50	x	.
Mistle Thrush	*Turdus viscivorus*	115.00	.	x
American Kestrel	*Falco sperverius*	115.50	x	.
Mourning Dove	*Zeneide macroura*	119.00	x	.
Northern Flicker	*Coleptes auretus*	132.00	x	.
Boreal Owl	*Aegolius funereus*	134.00	x	.
Tengmelm's Owl	*Aegolius funereus*	134.00	.	x
Grey-headed Woodpecker	*Picus canus*	137.00	.	x
Sharp-shinned Hawk	*Accipiter strietus*	138.50	x	.
Collared Dove	*Streptopelia deceoto*	149.00	.	x
Burrowing Owl	*Athene cuniculerie*	155.00	x	.
Corncrake	*Crex crex*	155.50	.	x
Jay	*Garrulus glenderius*	161.00	.	x
Red-footed Falcon	*Falco vespertinus*	165.50	.	x
Nutcracker	*Nucifrage caryocatactes*	172.50	.	x
Magpie	*Pica pice*	177.50	.	x
Merlin	*Falco columbarius*	185.50	x	.
Kestrel	*Falco tinnunculus*	201.50	.	x
Lapwing	*Vanellus vanellus*	218.50	.	x
Sparrowhawk	*Accipitar nisus*	237.50	.	x
Hobby	*Falco subbuteo*	240.00	.	x
Jackdaw	*Corvus monedula*	246.00	.	x
Long-eared Owl	*Asio otus*	262.00	x	x
Pileated Woodpecker	*Dryocopus pileatus*	287.00	x	.
Stock Dove	*Columba oenas*	291.00	.	x
Woodcock	*Scolopax rusticole*	309.50	.	x
Black Woodpecker	*Dryocopus martius*	321.00	.	x
Hawk owl	*Surnia ulule*	322.00	x	x
Teal	*Anas crecca*	341.00	.	x
Grey Partridge	*Perdix perdix*	389.50	x	x
Hazelhen	*Bonasa bonasia*	429.00	.	x
Cooper's Hawk	*Accipiter cooperii*	439.00	x	.
Northern Harrier	*Circus cyaneus*	440.50	x	.
American Crow	*Corvus brachyrhynchos*	448.00	x	.
Broad-winged Hawk	*Buteo platypterus*	455.00	x	.
Spruce Grouse	*Dendragapus canadensis*	474.00	x	.
Tawny Owl	*Strix aluco*	475.00	.	x
Rook	*Corvus frugilegus*	488.00	.	x
Woodpigeon	*Columba palumbus*	490.00	.	x
Rock Dove	*Columba livia*	542.00	.	x
Willow Ptermigan/Grouse	*Lagopus lagopus*	558.50	x	x

Common name	Scientific name	Body Mass (g)	New World	Old World
Hooded Crow	*Corvus corone cornix*	570.00	.	x
Ruffed Grouse	*Bonasa umbellus*	576.50	x	.
Honey Buzzard	*Pernis apivorus*	758.00	.	x
Wigeon	*Anas penelope*	771.50	.	x
Ural Owl	*Strix uralensis*	784.50	.	x
Curlew	*Numenius arquata*	805.50	.	x
Black Kite	*Milvus migrans*	827.00	.	x
Buzzard	*Buteo buteo*	875.00	.	x
Sharp-tailed Grouse	*Tympanuchus phasianellus*	885.00	x	.
Rough-legged Buzzard	*Buteo lagopus*	956.00	.	x
Goshawk	*Accipiter gentilis*	1024.50	.	x
Black Grouse	*Tetrao tetrix*	1082.50	.	x
Great Gray Owl	*Strix nebulosa*	1116.50	x	x
Red-tailed Hawk	*Buteo jamaicensis*	1126.00	x	.
Herring Gull	*Larus argentatus*	1135.00	.	x
Raven	*Corvus corax*	1199.00	x	x
Great Horned Owl	*Bubo virginianus occidentalis*	1354.50	x	.
Great Horned Owl	*Bubo virginianus virginianus*	1543.50	x	.
Spotted Eagle	*Aquila clanga*	2205.50	.	x
Eagle Owl	*Bubo bubo*	2686.00	.	x
Capercaillie	*Tetrao urogallus*	2950.00	.	x
Sandhill Crane	*Grus canadensis canadensis*	3166.00	x	.
Golden Eagle	*Aquila chrysaetos*	4195.00	x	x

APPENDIX D
SITES AND DATES OF SURVEYS USED IN SUMMER AND SPRING DATA LISTS

Census Sites	Dates (Summer)
Chicago IL	
Lake Forest	June 1974, June/July 1975, June 1976, June 1977
Skokie	June/July 1974, July 1975, June/July 1976, June 1977
South Evanston	June/July 1976, June 1977
N. C. Chicago	June 1974, June/July 1975, June 1976, June 1977
Addison	June 1974, June 1975
North Evanston	June 1975, June 1976
Wilmette	June 1974, June/July 1975, June 1976, June/July 1977
Winnetka	June 1974, June/July 1975, June 1976, June/July 1977
Amherst MA	
OP	June 1975 and June 1976
MT	June 1975 and June 1976
YT	June 1975 and June 1976
Springfield MA	
All Sites	June 1975 and June 1976
Austin TX	
French Place	March/May 1976
Hyde Park	March/April/May/June 1976
Tarrytown	April/May/June 1976, March/April/June 1977
Blacksburg VA	
Airport Acres	May/June/July 1973
Blackwood	May/June/July 1973
Draper Preston	May/June/July 1973
McBryde Vill.	May/June/July 1973
Highland Park	May/June/July 1973
Oak Manor	May/June/July 1973
Terrace View	May/June/July 1973
Vancouver(*l*)	
MacKenzie	June/July/August 1976
Collingwood	June/July/August 1976
Downtown	June/July/August 1976
False Creek	June/July/August 1976
Queen Elizabeth	June/July/August 1976
Shaughnessy	June/July/August 1976
West End	June/July/August 1976
Vancouver (*w*)	
Ferguson	June/July 1969
Churchill	June/July 1968, June/July 1969
Spruce	June/July 1968, June/July 1969
Yukon	June/July 1968, June/July 1969

l = Lancaster's study in Vancouver.
w = Weber's study in Vancouver.

Census Sites	Dates (Spring)
Chicago IL	
Lake Forest	May 1974
Skokie	May 1974, May 1975, May 1976
South Evanston	April/May 1976, April/May 1976
N. C. Chicago	April/May 1975
Addison	May 1974, April/May 1976
Wilmette	May 1975
Seattle WA	
Ballard	April 15 - June 15 1980, April 15 - June 15 1981
Central	April 15 - June 15 1980, April 15 - June 15 1981
Madronna	April 15 - June 15 1980, April 15 - June 15 1981
North End	April 15 - June 15 1980, April 15 - June 15 1981
Queen Ann	April 15 - June 15 1980, April 15 - June 15 1981
Ravenna	April 15 - June 15 1980, April 15 - June 15 1981
Vancouver BC(*l*)	
MacKenzie	April 11 - May 31 1976
Collingwood	April 11 - May 31 1976
Downtown	April 11 - May 31 1976
False Creek	April 11 - May 31 1976
Queen Elizabeth	April 11 - May 31 1976
Shaughnessy	April 11 - May 31 1976
West End	April 11 - May 31 1976
Vancouver (*w*)	
Ferguson	April/May 1969
Churchill	April/May 1968, April/May 1969
Spruce	April/May 1968, April/May 1969
Yukon	April/May 1968, April/May 1969

l = Lancaster's study in Vancouver.
w = Weber's study in Vancouver.

APPENDIX E
SUBURBAN SPRING BIRD SURVEYS

Standardized spring surveys. Species, range status (B = breeding, R = resident, Migrant = birds that migrate through a suburban area but do not breed), mass (grams), and bird counts (# of birds/hour) are reported for bird censuses conducted in cities across North America. All birds are characterized as primarily tree canopy users*.

SPECIES	STATUS	WT. (g)	SUBURBAN BIRD CENSUS SITES						
			Chicago	Chicago	Chicago	Chicago	Chicago	Chicago	Vanc (L*)
			Lake Forest	Addison	NC. Chic	S. Evas	Skokie	Wilm	CW
Ruby-throated Hummingbird	B	3.15							
Rufous Hummingbird (*a*)	B	3.25							
Bushtit	R	5.30							
Golden-crowned Kinglet (*b*)	R	6.20				0.125			
Lucy's Warbler	B	6.60							
Ruby-crowned Kinglet (*c*)	B	6.65	1.200		2.000	1.875	0.692	0.741	0.285
Wilson's Warbler (*d*)	B	6.90				0.125			1.872
American Redstart	B	8.30	0.400		0.500	0.125	0.462	0.370	
Black-throated Gray Warbler	B	8.35							
Blue-winged Warbler	B	8.40							
Brown Creeper	R	8.40				0.125			
Magnolia Warbler	B	8.70				0.125	0.692		
Black-throated Green Warbler	B	8.80	0.200			0.125	0.923	0.185	
Townsend's Warbler	B	8.85							0.136
Winter Wren	R	8.90							
Orange-crowned Warbler	B	9.00							
Yellow Warbler (*e*)	B	9.50				0.125			0.374
Chestnut-sided Warbler	B	9.60	0.400			0.125	0.231	0.185	
Chestnut-backed Chickadee	R	9.70							
Blackburnian Warbler	B	9.75				0.375	0.231	0.370	
Red-breasted Nuthatch	R	9.80							
Bewick's Wren	R	9.90							
Tennessee Warbler	Migrant	10.00	0.200		0.500	0.125	1.385	0.556	
Least Flycatcher	B	10.30	0.800	0.250	0.500			0.556	
Canada Warbler	B	10.40	0.200				0.692	0.370	
MacGillivray's Warbler	B	10.40							
Black-and-white Warbler	B	10.80							
Black-capped Chickadee (*f*)	B	10.80	1.600					0.185	0.071
Western Flycatcher	B	10.90							
Cape May Warbler	Migrant	11.00				0.130			
White-eyed Vireo	B	11.40						0.185	
Yellow-bellied Flycatcher	B	11.60	0.200						
Warbling Vireo	B	12.00							0.385
Mourning Warbler	B	12.50							
Yellow-rumped Warbler (*g*)	R	12.55	0.400				1.385	0.556	0.071
Bay-breasted Warbler	Migrant	12.55				0.250		0.741	
Western Wood-Pewee	B	12.80							
American Goldfinch	R	12.90	0.200	2.500		0.125	0.231		1.019
Blackpoll Warbler	B	13.00	0.200			0.125	0.231	2.222	
Willow Flycatcher	B	13.40				0.125	0.231		
Kentucky Warbler	B	14.00	0.200			0.125			
Eastern Wood-Pewee	B	14.10	1.000				0.462	0.556	
Indigo Bunting	B	14.50	1.400					0.741	
Pine Siskin	R	14.60							
Solitary Vireo	B	16.60							
Red-eyed Vireo	B	16.70	4.800	1.250		0.125	1.385	4.444	
Yellow-throated Vireo	B	18.00	0.200				0.231		
Dark-eyed Junco	R	19.60			1.000	0.625		0.185	
Eastern Phoebe	R	19.80							
Tree Swallow	B	20.10							

SPECIES	STATUS	WT. (g)	SUBURBAN BIRD CENSUS SITES						
			Chicago	Chicago	Chicago	Chicago	Chicago	Chicago	Vanc (L*)
			Lake Forest	Addison	NC. Chic	S. Evas	Skokie	Wilm	CW
White-breasted Nuthatch	R	21.10	0.400						
Tufted Titmouse	R	21.60							
Downy Woodpecker (*h*)	R	27.00	0.500	0.125				0.278	
Western Tanager	B	28.10							0.385
Scarlet Tanager	B	28.60							
Swainson's Thrush	B	30.80	1.800		2.500	1.375	2.077	1.481	
Hermit Thrush	R	31.00	0.200		0.500	0.125			
Veery	B	31.20	0.200				0.231		
Cedar Waxwing	R	31.85				0.625			
Olive-sided Flycatcher	B	32.10							
Great Crested Flycatcher	B	33.50	0.200						
Northern Oriole	R	33.75	4.000			0.375		0.741	
Townsend's Solitaire	R	34.00							
Red Crossbill	R	36.50							
Gray Catbird	B	36.90	0.600	0.250		0.125	0.462	0.185	
Cactus Wren	R	38.90							
Eastern Kingbird	B	39.50						0.370	
Western Kingbird	B	39.60							
Black-headed Grosbeak	B	44.50							
Rose-breasted Grosbeak	B	45.60	2.400	0.250	1.000	1.375	0.462	2.407	
Wood Thrush	B	47.40							
Yellow-bellied Sapsucker	B	50.30	0.200						
Black-billed Cuckoo	B	51.10	0.600						
Red-bellied Woodpecker	R	61.70							
Yellow-billed Cuckoo	B	64.00	0.400				0.231		
Hairy Woodpecker	R	66.25	0.400						
Brown Thrasher	B	68.80	0.600		0.500	0.125			
Red-headed Woodpecker	R	71.60						0.926	
Varied Thrush	R	78.40							
Curved-billed Thrasher	R	79.40							
Golden-fronted Woodpecker	R	80.90							
Steller's Jay	R	106.00							
Northern Flicker	R	132.00	1.600			0.875		0.556	
Pileated Woodpecker	R	287.00							
Band-tailed Pigeon	B	342.50							
Northwestern Crow	R	391.50							0.249
American Crow	R	448.00							

SPECIES	STATUS	WT. (g)	SUBURBAN BIRD CENSUS SITES							
			Vanc (L*) MK	Vanc (L*) DT	Vanc (L*) FC	Vanc (L*) QE	Vanc (L*) SH	Vanc (L*) WE	Seattle North End	Seattle Ravenna
Ruby-throated Hummingbird	B	3.15								
Rufous Hummingbird (*a*)	B	3.25							0.138	
Bushtit	R	5.30							3.923	3.139
Golden-crowned Kinglet (*b*)	R	6.20							0.138	0.062
Lucy's Warbler	B	6.60								
Ruby-crowned Kinglet (*c*)	B	6.65					0.479			
Wilson's Warbler (*d*)	B	6.90	0.023			0.109	1.743	0.030	0.231	0.069
American Redstart	B	8.30								
Black-throated Gray Warbler	B	8.35								
Blue-winged Warbler	B	8.40								
Brown Creeper	R	8.40								
Magnolia Warbler	B	8.70								
Black-throated Green Warbler	B	8.80								
Townsend's Warbler	B	8.85								
Winter Wren	R	8.90								
Orange-crowned Warbler	B	9.00					0.657		0.646	0.508
Yellow Warbler (*e*)	B	9.50	0.068				0.170			
Chestnut-sided Warbler	B	9.60								
Chestnut-backed Chickadee	R	9.70							1.523	
Blackburnian Warbler	B	9.75								
Red-breasted Nuthatch	R	9.80							3.231	
Bewick's Wren	R	9.90							0.231	
Tennessee Warbler	Migrant	10.00								
Least Flycatcher	B	10.30								
Canada Warbler	B	10.40								
MacGillivray's Warbler	B	10.40					0.340			
Black-and-white Warbler	B	10.80								
Black-capped Chickadee (*f*)	B	10.80	0.071				0.712		1.411	0.989
Western Flycatcher	B	10.90								
Cape May Warbler	Migrant	11.00								
White-eyed Vireo	B	11.40								
Yellow-bellied Flycatcher	B	11.60								
Warbling Vireo	B	12.00								0.092
Mourning Warbler	B	12.50								
Yellow-rumped Warbler (*g*)	R	12.55					0.097		0.158	0.171
Bay-breasted Warbler	Migrant	12.55								
Western Wood-Pewee	B	12.80								
American Goldfinch	R	12.90				1.290	0.181	0.181	0.046	
Blackpoll Warbler	B	13.00								
Willow Flycatcher	B	13.40								
Kentucky Warbler	B	14.00								
Eastern Wood-Pewee	B	14.10								
Indigo Bunting	B	14.50								
Pine Siskin	R	14.60							4.339	1.708
Solitary Vireo	B	16.60								
Red-eyed Vireo	B	16.70					0.158			
Yellow-throated Vireo	B	18.00								
Dark-eyed Junco	R	19.60							0.646	0.369
Eastern Phoebe	R	19.80								
Tree Swallow	B	20.10								

SPECIES	STATUS	WT. (g)	SUBURBAN BIRD CENSUS SITES							
			Vanc (L*) MK	Vanc (L*) DT	Vanc (L*) FC	Vanc (L*) QE	Vanc (L*) SH	Vanc (L*) WE	Seattle North End	Seattle Ravenna
White-breasted Nuthatch	R	21.10								
Tufted Titmouse	R	21.60								
Downy Woodpecker (*h*)	R	27.00								0.185
Western Tanager	B	28.10							0.138	
Scarlet Tanager	B	28.60								
Swainson's Thrush	B	30.80								
Hermit Thrush	R	31.00								0.092
Veery	B	31.20								
Cedar Waxwing	R	31.85								
Olive-sided Flycatcher	B	32.10					0.498		0.092	
Great Crested Flycatcher	B	33.50								
Northern Oriole	R	33.75								
Townsend's Solitaire	R	34.00								
Red Crossbill	R	36.50							1.200	
Gray Catbird	B	36.90								
Cactus Wren	R	38.90								
Eastern Kingbird	B	39.50								
Western Kingbird	B	39.60								
Black-headed Grosbeak	B	44.50							0.092	
Rose-breasted Grosbeak	B	45.60								
Wood Thrush	B	47.40								
Yellow-bellied Sapsucker	B	50.30								
Black-billed Cuckoo	B	51.10								
Red-bellied Woodpecker	R	61.70								
Yellow-billed Cuckoo	B	64.00								
Hairy Woodpecker	R	66.25								
Brown Thrasher	B	68.80								
Red-headed Woodpecker	R	71.60								
Varied Thrush	R	78.40					0.498			
Curved-billed Thrasher	R	79.40								
Golden-fronted Woodpecker	R	80.90								
Steller's Jay	R	106.00							0.462	
Northern Flicker	R	132.00	0.136						0.138	
Pileated Woodpecker	R	287.00								
Band-tailed Pigeon	B	342.50							4.154	0.508
Northwestern Crow	R	391.50	0.136	0.566		0.317	2.988			
American Crow	R	448.00							8.031	4.662

SPECIES	STATUS	WT. (g)	SUBURBAN BIRD CENSUS SITES							
			Seattle Ballard	Seattle Central	Seattle Madron	Seattle Queen Anne	Vanc W* Church	Vanc W* Fergus	Vanc W* Spruce	Vanc W* Yukon
Ruby-throated Hummingbird	B	3.15								
Rufous Hummingbird (*a*)	B	3.25		0.185			0.540	0.103	0.081	0.392
Bushtit	R	5.30	4.339	5.354	3.415	1.431	1.140			
Golden-crowned Kinglet (*b*)	R	6.20	0.031		0.308	0.046	0.660	0.034	0.027	0.026
Lucy's Warbler	B	6.60								
Ruby-crowned Kinglet (*c*)	B	6.65					1.680	0.117	0.232	1.120
Wilson's Warbler (*d*)	B	6.90	0.223	0.285	0.085	0.269	0.290	0.051	0.027	0.078
American Redstart	B	8.30								
Black-throated Gray Warbler	B	8.35					0.060			
Blue-winged Warbler	B	8.40								
Brown Creeper	R	8.40								
Magnolia Warbler	B	8.70								
Black-throated Green Warbler	B	8.80								
Townsend's Warbler	B	8.85					0.120	0.103		
Winter Wren	R	8.90					0.060			
Orange-crowned Warbler	B	9.00	0.092	0.646		0.277	0.060	0.103	0.163	0.314
Yellow Warbler (*e*)	B	9.50			0.069		0.210	0.154	0.041	0.157
Chestnut-sided Warbler	B	9.60								
Chestnut-backed Chickadee	R	9.70			0.369					
Blackburnian Warbler	B	9.75								
Red-breasted Nutbatch	R	9.80	0.092	2.123			0.060			
Bewick's Wren	R	9.90		0.185	0.323					
Tennessee Warbler	Migrant	10.00								
Least Flycatcher	B	10.30								
Canada Warbler	B	10.40								
MacGillivray's Warbler	B	10.40		0.277	0.138		0.120		0.081	0.157
Black-and-white Warbler	B	10.80								
Black-capped Chickadee (*f*)	B	10.80	0.409	1.147	0.884		1.251		0.116	0.336
Western Flycatcher	B	10.90					0.060			
Cape May Warbler	Migrant	11.00								
White-eyed Vireo	B	11.40								
Yellow-bellied Flycatcher	B	11.60								
Warbling Vireo	B	12.00					0.540			
Mourning Warbler	B	12.50								
Yellow-rumped Warbler (*g*)	R	12.55	0.224	1.398	0.105		1.629	0.176	0.046	0.179
Bay-breasted Warbler	Migrant	12.55								
Western Wood-Pewee	B	12.80					0.180			
American Goldfinch	R	12.90			0.969		3.780	0.514	0.163	1.020
Blackpoll Warbler	B	13.00								
Willow Flycatcher	B	13.40								
Kentucky Warbler	B	14.00								
Eastern Wood-Pewee	B	14.10								
Indigo Bunting	B	14.50								
Pine Siskin	R	14.60	0.092	1.292	0.877	0.785	3.600			
Solitary Vireo	B	16.60		0.277						
Red-eyed Vireo	B	16.70								
Yellow-throated Vireo	B	18.00								
Dark-eyed Junco	R	19.60		0.138		0.138	2.700			
Eastern Phoebe	R	19.80								
Tree Swallow	B	20.10						0.514		

SPECIES	STATUS	WT. (g)	SUBURBAN BIRD CENSUS SITES							
			Seattle Ballard	Seattle Central	Seattle Madron	Seattle Queen Anne	Vanc W* Churcb	Vanc W* Fergus	Vanc W* Spruce	Vanc W* Yukon
White-breasted Nuthatch	R	21.10								
Tufted Titmouse	R	21.60								
Downy Woodpecker (*h*)	R	27.00				0.138				
Western Tanager	B	28.10					0.300	0.103		
Scarlet Tanager	B	28.60								
Swainson's Thrush	B	30.80								
Hermit Thrush	R	31.00	0.092	0.277	0.138		0.600	0.103		0.392
Veery	B	31.20								
Cedar Waxwing	R	31.85	0.092			1.523	1.140			
Olive-sided Flycatcher	B	32.10		0.646			0.060			
Great Crested Flycatcher	B	33.50								
Northern Oriole	R	33.75								
Townsend's Solitaire	R	34.00					0.060			
Red Crossbill	R	36.50								
Gray Catbird	B	36.90								
Cactus Wren	R	38.90								
Eastern Kingbird	B	39.50								
Western Kingbird	B	39.60								
Black-headed Grosbeak	B	44.50		0.785		0.369				
Rose-breasted Grosbeak	B	45.60								
Wood Thrush	B	47.40								
Yellow-bellied Sapsucker	B	50.30								
Black-billed Cuckoo	B	51.10								
Red-bellied Woodpecker	R	61.70								
Yellow-billed Cuckoo	B	64.00								
Hairy Woodpecker	R	66.25								
Brown Thrasher	B	68.80								
Red-headed Woodpecker	R	71.60								
Varied Thrush	R	78.40					0.660		0.081	0.235
Curved-billed Thrasher	R	79.40								
Golden-fronted Woodpecker	R	80.90								
Steller's Jay	R	106.00					0.180			
Northern Flicker	R	132.00					0.060			
Pileated Woodpecker	R	287.00								
Band-tailed Pigeon	B	342.50	0.092	3.739	0.646	0.415	6.600	0.925		
Northwestern Crow	R	391.50					1.800		0.244	0.157
American Crow	R	448.00	3.969	4.892	6.277	2.169				

a Rufous hummingbirds censused in Seattle and Vancouver were standardized from BBC counts by dividng the bird density at each site by 2.0. This is because the Rufous hummingbird was 2 times more abundant in Seattle and Vancouver than the Ruby-throated hummingbird in Chicago, Amherst, and Blacksburg.

b Golden-crowned kinglets censused in Seattle and Vancouver were standardized from BBC counts by dividng the bird density at each site by 3.0.

c Ruby-crowned kinglets censused in Seattle and Vancouver were standardized from BBC counts by dividng the bird density at each site by 1.75.

d Wilson's warblers censused in Seattle and Vancouver were standardized from BBC counts by dividng the bird density at each site by 6.0.

e Yellow warblers censused in Seattle and Vancouver were standardized from BBC counts by dividng the bird density at each site by 2.0.

f Black-capped chickadees censused in Seattle and Vancouver were standardized from BBC counts by dividng the bird density at each site by 3.5.

g Yellow-rumped warblers censused in Seattle and Vancouver were standardized from BBC counts by dividng the bird density at each site by 3.5.

h Downy woodpeckers censused in Chicago were standardized from BBC counts by dividng the bird density at each site by 2.0.

* excluding exotics, urban adapted birds (cardinal, blue jay, common grackle, mourning dove, chipping sparrow, mockingbird, house finch, cowbird, house wren, great-tailed grackle), and a few birds that were sighted in the surveys but left out because they foraged primarily on the ground (rufous-sided towhee, purple finch).

L* Lancaster's study in Vancouver

W* Weber's study in Vancouver

APPENDIX F
SUBURBAN SUMMER BIRD SURVEYS

Standardized Summer Surveys. Species, range status (B = breeding, R = resident), bird densities (# of birds/hour) are reported for bird censuses conducted in cities across North America. All birds are characterized as primarily tree canopy users*.

SPECIES	STATUS	WT. (g)	SUBURBAN BIRD CENSUS SITES						
			Amherst MT	Amherst OP	Amherst YT	Austin FP	Austin HP	Austin T	Spring field
Ruby-throated Hummingbird	B	3.15	0.100	0.050					0.050
Rufous Hummingbird *a*	B	3.25							
Bushtit	R	5.30							
Golden-crowned Kinglet *b*	R	6.20							
American Redstart	B	8.30	0.250						
Blue-winged Warbler	B	8.40		0.050					
Brown Creeper	R	8.40	0.100						
Lesser Goldfinch	R	9.50							
Yellow Warbler *e*	B	9.50	0.550						
Red-breasted Nuthatch	R	9.80	0.100	0.050					0.025
Bewick's Wren	R	9.90							
Carolina Chickadee	R	10.15				1.598	1.022	3.500	
Least Flycatcher	B	10.30							
Black-and-white Warbler	B	10.80							
Black-capped Chickadee *f*	B	10.80	0.700	1.750	0.075				0.125
Warbling Vireo	B	12.00		0.050					
American Goldfinch	R	12.90		0.350					
Blackpoll Warbler	B	13.00	0.200	0.050					
Willow Flycatcher	B	13.40							
Eastern Wood-Pewee	B	14.10	0.100	0.650					
Indigo Bunting	B	14.50							
Pine Siskin	R	14.60							
Red-eyed Vireo	B	16.70	0.550	1.550					0.050
Eastern Phoebe	R	19.80		1.750					
Tree Swallow	B	20.10		0.450	2.500				
Carolina Wren	R	21.00						0.260	
White-breasted Nuthatch	R	21.10	0.450	1.650					
Tufted Titmouse	R	21.60		1.400				3.761	0.100
Purple Finch	R	24.90							
Downy Woodpecker *h*	R	27.00	0.050	0.550	0.050				0.025
Western Tanager	B	28.10							
Scarlet Tanager	B	28.60	0.200	0.750					
Swainson's Thrush	B	30.80	0.100	0.150					
Hermit Thrush	R	31.00		0.050					
Cedar Waxwing	R	31.85							
Great Crested Flycatcher	B	33.50		0.200		1.067	1.358	1.039	
Northern Oriole	R	33.75	0.350	4.200	0.200				0.525
Gray Catbird	B	36.90	4.200	1.450	1.050				0.050
Eastern Kingbird	B	39.50		0.100	0.300				
Rufous-sided Towhee	R	40.50	0.050	0.550					
Black-headed Grosbeak	B	44.50							
Rose-breasted Grosbeak	B	45.60	0.250	0.200					
Wood Thrush	B	47.40	0.950	3.050					
Black-billed Cuckoo	B	51.10							
Evening Grosbeak	R	59.40							
Red-bellied Woodpecker	R	61.70				1.242	4.760	3.698	
Yellow-billed Cuckoo	B	64.00					1.385	0.388	
Hairy Woodpecker	R	66.25	0.300	0.700					

SPECIES	STATUS	WT. (g)	SUBURBAN BIRD CENSUS SITES						
			Amherst MT	Amherst OP	Amherst YT	Austin FP	Austin HP	Austin T	Spring field
Brown Thrasher	B	68.80	0.500	0.050					
Red-headed Woodpecker	R	71.60							
Golden-fronted Woodpecker	R	80.90						1.233	
Northern Flicker	R	132.00	0.150	1.000	0.050				
Band-tailed Pigeon	B	342.50							
Northwestern Crow	R	391.50							
American Crow	R	448.00	0.550	0.350					0.150

SPECIES	STATUS	WT. (g)	SUBURBAN BIRD CENSUS SITES						
			Black Highlan	Black Airport	Black Draper	Black Terrace	Black McBryd	Black Oak	Black Blackw
Ruby-throated Hummingbird	B	3.15							
Rufous Hummingbird *a*	B	3.25							
Bushtit	R	5.30							
Golden-crowned Kinglet *b*	R	6.20							
American Redstart	B	8.30							
Blue-winged Warbler	B	8.40							
Brown Creeper	R	8.40							
Lesser Goldfinch	R	9.50							
Yellow Warbler *e*	B	9.50	0.238	0.714			0.238		
Red-breasted Nuthatch	R	9.80							
Bewick's Wren	R	9.90							
Carolina Chickadee	R	10.15		0.238	2.143			2.143	0.952
Least Flycatcher	B	10.30							
Black-and-white Warbler	B	10.80							
Black-capped Chickadee *f*	B	10.80							
Warbling Vireo	B	12.00							
American Goldfinch	R	12.90		0.952				0.238	
Blackpoll Warbler	B	13.00							
Willow Flycatcher	B	13.40							
Eastern Wood-Pewee	B	14.10							2.143
Indigo Bunting	B	14.50							
Pine Siskin	R	14.60							
Red-eyed Vireo	B	16.70	0.238						
Eastern Phoebe	R	19.80							
Tree Swallow	B	20.10							
Carolina Wren	R	21.00							
White-breasted Nuthatch	R	21.10						0.714	
Tufted Titmouse	R	21.60	0.714		0.238			1.191	0.238
Purple Finch	R	24.90							
Downy Woodpecker *h*	R	27.00						0.159	0.317
Western Tanager	B	28.10							
Scarlet Tanager	B	28.60						0.476	0.238
Swainson's Thrush	B	30.80							
Hermit Thrush	R	31.00							
Cedar Waxwing	R	31.85							1.191
Great Crested Flycatcher	B	33.50						2.143	0.476
Northern Oriole	R	33.75	2.381	0.238	0.238			2.143	2.381
Gray Catbird	B	36.90	0.952		0.476				1.429
Eastern Kingbird	B	39.50							
Rufous-sided Towhee	R	40.50	0.714		0.238				4.048
Black-headed Grosbeak	B	44.50							
Rose-breasted Grosbeak	B	45.60							
Wood Thrush	B	47.40							
Black-billed Cuckoo	B	51.10							
Evening Grosbeak	R	59.40							
Red-bellied Woodpecker	R	61.70						0.238	
Yellow-billed Cuckoo	B	64.00							
Hairy Woodpecker	R	66.25							

SPECIES	STATUS	WT. (g)	SUBURBAN BIRD CENSUS SITES						
			Black Highlan	Black Airport	Black Draper	Black Terrace	Black McBryd	Black Oak	Black Blackwo
Brown Thrasher	B	68.80			1.667				2.857
Red-headed Woodpecker	R	71.60	0.238						
Golden-fronted Woodpecker	R	80.90							
Northern Flicker	R	132.00			0.238			0.476	1.667
Band-tailed Pigeon	B	342.50							
Northwestern Crow	R	391.50							
American Crow	R	448.00							

SPECIES	STATUS	WT. (g)	SUBURBAN BIRD CENSUS SITES						
			Chicago Lake For	Chicago Addis	Chicago NCCH	Chicago NEVA	Chicago SEVA	Chicago Skok	Chicago Wilm
Ruby-throated Hummingbird	B	3.15	0.144						
Rufous Hummingbird *a*	B	3.25							
Bushtit	R	5.30							
Golden-crowned Kinglet *b*	R	6.20							
American Redstart	B	8.30							
Blue-winged Warbler	B	8.40							
Brown Creeper	R	8.40							
Lesser Goldfinch	R	9.50							
Yellow Warbler *e*	B	9.50							
Red-breasted Nuthatch	R	9.80							
Bewick's Wren	R	9.90							
Carolina Chickadee	R	10.15							
Least Flycatcher	B	10.30	0.144						
Black-and-white Warbler	B	10.80						0.130	
Black-capped Chickadee *f*	B	10.80	11.095			3.283	0.728		1.684
Warbling Vireo	B	12.00							
American Goldfinch	R	12.90		0.938					
Blackpoll Warbler	B	13.00							
Willow Flycatcher	B	13.40	0.144					0.391	
Eastern Wood-Pewee	B	14.10	0.144			0.313			0.321
Indigo Bunting	B	14.50	1.875						
Pine Siskin	R	14.60							
Red-eyed Vireo	B	16.70				1.875		0.391	0.401
Eastern Phoebe	R	19.80							
Tree Swallow	B	20.10	1.442						
Carolina Wren	R	21.00							
White-breasted Nuthatch	R	21.10	0.289						0.321
Tufted Titmouse	R	21.60							
Purple Finch	R	24.90							
Downy Woodpecker *h*	R	27.00	0.865					0.130	0.321
Western Tanager	B	28.10							
Scarlet Tanager	B	28.60							0.080
Swainson's Thrush	B	30.80							
Hermit Thrush	R	31.00							
Cedar Waxwing	R	31.85				0.313		0.261	2.246
Great Crested Flycatcher	B	33.50	1.298		0.100	0.938			0.241
Northern Oriole	R	33.75	2.740						2.166
Gray Catbird	B	36.90	1.298					0.261	0.160
Eastern Kingbird	B	39.50	0.144						
Rufous-sided Towhee	R	40.50							
Black-headed Grosbeak	B	44.50							
Rose-breasted Grosbeak	B	45.60	1.298			0.625		0.261	0.561
Wood Thrush	B	47.40							
Black-billed Cuckoo	B	51.10	0.144						
Evening Grosbeak	R	59.40							
Red-bellied Woodpecker	R	61.70	0.144						
Yellow-billed Cuckoo	B	64.00	0.289			0.313		0.130	0.160
Hairy Woodpecker	R	66.25	0.289						0.080

SPECIES	STATUS	WT. (g)	SUBURBAN BIRD CENSUS SITES						
			Black Highlan	Black Airport	Black Draper	Black Terrace	Black McBryd	Black Oak	Black Blackwo
Brown Thrasher	B	68.80	0.144						0.080
Red-headed Woodpecker	R	71.60							1.283
Golden-fronted Woodpecker	R	80.90							
Northern Flicker	R	132.00	1.731			0.625	0.208		0.241
Band-tailed Pigeon	B	342.50							
Northwestern Crow	R	391.50							
American Crow	R	448.00							

SPECIES	STATUS	WT. (g)	SUBURBAN BIRD CENSUS SITES						
			Chicago Lake For	Chicago Addis	Chicago NCCH	Chicago NEVA	Chicago SEVA	Chicago Skok	Chicago Wilm
Ruby-throated Hummingbird	B	3.15	0.144						
Rufous Hummingbird *a*	B	3.25							
Bushtit	R	5.30							
Golden-crowned Kinglet *b*	R	6.20							
American Redstart	B	8.30							
Blue-winged Warbler	B	8.40							
Brown Creeper	R	8.40							
Lesser Goldfinch	R	9.50							
Yellow Warbler *e*	B	9.50							
Red-breasted Nuthatch	R	9.80							
Bewick's Wren	R	9.90							
Carolina Chickadee	R	10.15							
Least Flycatcher	B	10.30	0.144						
Black-and-white Warbler	B	10.80						0.130	
Black-capped Chickadee *f*	B	10.80	11.095			3.283	0.728		1.684
Warbling Vireo	B	12.00							
American Goldfinch	R	12.90		0.938					
Blackpoll Warbler	B	13.00							
Willow Flycatcher	B	13.40	0.144					0.391	
Eastern Wood-Pewee	B	14.10	0.144			0.313			0.321
Indigo Bunting	B	14.50	1.875						
Pine Siskin	R	14.60							
Red-eyed Vireo	B	16.70				1.875		0.391	0.401
Eastern Phoebe	R	19.80							
Tree Swallow	B	20.10	1.442						
Carolina Wren	R	21.00							
White-breasted Nuthatch	R	21.10	0.289						0.321
Tufted Titmouse	R	21.60							
Purple Finch	R	24.90							
Downy Woodpecker	R	27.00	0.865					0.130	0.321
Western Tanager	B	28.10							
Scarlet Tanager	B	28.60							0.080
Swainson's Thrush	B	30.80							
Hermit Thrush	R	31.00							
Cedar Waxwing	R	31.85				0.313		0.261	2.246
Great Crested Flycatcher	B	33.50	1.298		0.100	0.938			0.241
Northern Oriole	R	33.75	2.740						2.166
Gray Catbird	B	36.90	1.298					0.261	0.160
Eastern Kingbird	B	39.50	0.144						
Rufous-sided Towhee	R	40.50							
Black-headed Grosbeak	B	44.50							
Rose-breasted Grosbeak	B	45.60	1.298			0.625		0.261	0.561
Wood Thrush	B	47.40							
Black-billed Cuckoo	B	51.10	0.144						
Evening Grosbeak	R	59.40							
Red-bellied Woodpecker	R	61.70	0.144						
Yellow-billed Cuckoo	B	64.00	0.289			0.313		0.130	0.160
Hairy Woodpecker	R	66.25	0.289						0.080

SPECIES	STATUS	WT. (g)	SUBURBAN BIRD CENSUS SITES						
			Chicago Lake For	Chicago Addis	Chicago NOCH	Chicago NEVA	Chicago SEVA	Chicago Skok	Chicago Wilm
Brown Thrasher	B	68.80	0.144						0.080
Red-headed Woodpecker	R	71.60							1.283
Golden-fronted Woodpecker	R	80.90							
Northern Flicker	R	132.00	1.731			0.625	0.208		0.241
Band-tailed Pigeon	B	342.50							
Northwestern Crow	R	391.50							
American Crow	R	448.00							

SPECIES	STATUS	WT. (g)	SUBURBAN BIRD CENSUS SITES						
			Chicago Winn	Seattle CW	Seattle MK	Seattle DT	Seattle FC	Seattle QE	Seattle SH
Ruby-throated Hummingbird	B	3.15							
Rufous Hummingbird *a*	B	3.25			0.045				
Bushtit	R	5.30							
Golden-crowned Kinglet *b*	R	6.20							
American Redstart	B	8.30							
Blue-winged Warbler	B	8.40							
Brown Creeper	R	8.40							
Lesser Goldfinch	R	9.50							
Yellow Warbler *e*	B	9.50							
Red-breasted Nuthatch	R	9.80							
Bewick's Wren	R	9.90							
Carolina Chickadee	R	10.15							
Least Flycatcher	B	10.30							
Black-and-white Warbler	B	10.80							
Black-capped Chickadee *f*	B	10.80	5.250	4.181	1.582			1.062	9.673
Warbling Vireo	B	12.00							
American Goldfinch	R	12.90		0.520				0.203	0.271
Blackpoll Warbler	B	13.00							
Willow Flycatcher	B	13.40							0.090
Eastern Wood-Pewee	B	14.10	0.300						
Indigo Bunting	B	14.50	0.600						
Pine Siskin	R	14.60							
Red-eyed Vireo	B	16.70	1.500						
Eastern Phoebe	R	19.80							
Tree Swallow	B	20.10							
Carolina Wren	R	21.00							
White-breasted Nuthatch	R	21.10	0.300						
Tufted Titmouse	R	21.60							
Purple Finch	R	24.90		0.271				0.090	0.045
Downy Woodpecker *h*	R	27.00	1.500						
Western Tanager	B	28.10							
Scarlet Tanager	B	28.60							
Swainson's Thrush	B	30.80							
Hermit Thrush	R	31.00							
Cedar Waxwing	R	31.85							
Great Crested Flycatcher	B	33.50	2.400						
Northern Oriole	R	33.75	2.400						
Gray Catbird	B	36.90							
Eastern Kingbird	B	39.50	0.900						
Rufous-sided Towhee	R	40.50							
Black-headed Grosbeak	B	44.50							
Rose-breasted Grosbeak	B	45.60	2.700						
Wood Thrush	B	47.40							
Black-billed Cuckoo	B	51.10							
Evening Grosbeak	R	59.40							
Red-bellied Woodpecker	R	61.70							
Yellow-billed Cuckoo	B	64.00	0.300						
Hairy Woodpecker	R	66.25							

SPECIES	STATUS	WT. (g)	SUBURBAN BIRD CENSUS SITES						
			Chicago Winn	Seattle CW	Seattle MK	Seattle DT	Seattle FC	Seattle QE	Seattle SH
Brown Thrasher	B	68.80							
Red-headed Woodpecker	R	71.60	0.300						
Golden-fronted Woodpecker	R	80.90							
Northern Flicker	R	132.00	1.500						0.090
Band-tailed Pigeon	B	342.50		0.090					0.090
Northwestern Crow	R	391.50		0.181	0.497	0.565	0.407	0.294	2.034
American Crow	R	448.00							

SPECIES	STATUS	WT. (g)	SUBURBAN BIRD CENSUS SITES				
			Seattle WE	Vancouv Churchill	Vancouv Ferguson	Vancouv Spruce	Vancouv Yukon
Ruby-throated Hummingbird	B	3.15					
Rufous Hummingbird *a*	B	3.25					
Bushtit	R	5.30		0.164			
Golden-crowned Kinglet *b*	R	6.20		0.164			
American Redstart	B	8.30					
Blue-winged Warbler	B	8.40					
Brown Creeper	R	8.40		0.055			
Lesser Goldfinch	R	9.50					
Yellow Warbler *e*	B	9.50					
Red-breasted Nuthatch	R	9.80		0.218			0.064
Bewick's Wren	R	9.90		0.055			
Carolina Chickadee	R	10.15					
Least Flycatcher	B	10.30					
Black-and-white Warbler	B	10.80					
Black-capped Chickadee *f*	B	10.80	0.565	10.310	0.822	0.892	2.439
Warbling Vireo	B	12.00		0.491			
American Goldfinch	R	12.90		2.509	1.336	0.149	
Blackpoll Warbler	B	13.00					
Willow Flycatcher	B	13.40					
Eastern Wood-Pewee	B	14.10					
Indigo Bunting	B	14.50					
Pine Siskin	R	14.60	0.791	0.982			
Red-eyed Vireo	B	16.70					
Eastern Phoebe	R	19.80					
Tree Swallow	B	20.10					
Carolina Wren	R	21.00					
White-breasted Nuthatch	R	21.10					
Tufted Titmouse	R	21.60					
Purple Finch	R	24.90		0.164			
Downy Woodpecker *h*	R	27.00		0.165			
Western Tanager	B	28.10		0.273	0.103		
Scarlet Tanager	B	28.60					
Swainson's Thrush	B	30.80					
Hermit Thrush	R	31.00					
Cedar Waxwing	R	31.85					0.257
Great Crested Flycatcher	B	33.50					
Northern Oriole	R	33.75					
Gray Catbird	B	36.90					
Eastern Kingbird	B	39.50					
Rufous-sided Towhee	R	40.50					
Black-headed Grosbeak	B	44.50			0.103		
Rose-breasted Grosbeak	B	45.60					
Wood Thrush	B	47.40					
Black-billed Cuckoo	B	51.10					
Evening Grosbeak	R	59.40		0.109			
Red-bellied Woodpecker	R	61.70					
Yellow-billed Cuckoo	B	64.00					
Hairy Woodpecker	R	66.25					

SPECIES	STATUS	WT. (g)	SUBURBAN BIRD CENSUS SITES				
			Seattle WE	Vancouv Cburchill	Vancouv Ferguson	Vancouv Spruce	Vancouv Yukon
Brown Thrasher	B	68.80					
Red-headed Woodpecker	R	71.60					
Golden-fronted Woodpecker	R	80.90					
Northern Flicker	R	132.00					
Band-tailed Pigeon	B	342.50		0.327			
Northwestern Crow	R	391.50		1.309		0.744	
American Crow	R	448.00					

a Rufous hummingbirds censused in Seattle and Vancouver were standardized from BBC counts by dividng the bird density at each site by 2.0. This is because the Rufous hummingbird was 2 times more abundant in Seattle and Vancouver than the Ruby-throated hummingbird in Chicago, Amherst, and Blacksburg.

b Golden-crowned kinglets censused in Seattle and Vancouver were standardized from BBC counts by dividng the bird density at each site by 3.0.

c Ruby-crowned kinglets censused in Seattle and Vancouver were standardized from BBC counts by dividng the bird density at each site by 1.75.

d Wilson's warblers censused in Seattle and Vancouver were standardized from BBC counts by dividng the bird density at each site by 6.0.

e Yellow warblers censused in Seattle and Vancouver were standardized from BBC counts by dividng the bird density at each site by 2.0.

f Black-capped chickadees censused in Amherst and Springfield were standardized from BBC counts by dividng the bird density at each site by 2.0. Black-capped chickadee density in Chicago was multiplied by 3.5.

g Yellow-rumped warblers censused in Seattle and Vancouver were standardized from BBC counts by dividng the bird density at each site by 3.5.

h Downy woodpeckers censused in Blacksburg were standardized from BBC counts by dividng the bird density at each site by 1.5. Downy woodpecker densities in Vancouver and Seattle were multiplied by 3.0.

* excluding exotics, urban adapted birds (cardinal,blue jay, common grackle, mourning dove, chipping sparrow, mockingbird, house finch, cowbird, house wren, Great-tailed grackle), and a few birds that were sighted in the surveys but left out because they nest on the ground`(MacGillivray's warbler, Wilson's warbler, mourning warbler).

APPENDIX G
PERCENT TREE CANOPY COVER FOR SPRING SURVEY SITES

Percent tree canopy cover for different suburban sites at an area of 0.2 km^2 (Nominal scale = 1:2400). 1 pixel = 36.0 m^2.

City	Sites	CANOPY PATCH SIZE CATEGORIES										
		A	B	C	D	E	F	G	H	I	J	K
Chicago	Skokie	15.85	9.51	5.28	1.24	1.24	1.24	1.24	0.00	0.00	0.00	0.00
Chicago	S. Evanston	16.43	11.34	5.98	4.23	1.11	1.11	1.11	0.00	0.00	0.00	0.00
Chicago	Wilmette	46.19	44.73	40.87	36.34	32.60	29.56	27.49	26.34	24.94	23.45	23.45
Chicago	N.C. Chicago	3.09	1.08	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chicago	Lake Forest	43.42	42.39	38.02	37.13	33.98	33.98	32.00	29.69	29.69	29.69	29.69
Chicago	Addison	1.77	0.73	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Seattle	Ballard	8.63	1.42	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Seattle	Central	36.17	31.49	29.95	28.68	27.42	27.42	27.42	25.15	25.15	25.15	25.15
Seattle	Madronna	13.43	10.18	7.98	6.38	5.00	2.71	2.71	2.71	1.87	1.87	1.87
Seattle	Ravenna	11.60	6.76	2.00	0.80	0.80	0.00	0.00	0.00	0.00	0.00	0.00
Seattle	North End	25.24	19.75	15.15	14.82	13.62	12.11	12.11	12.11	12.11	12.11	12.11
Seattle	Q. Anne	8.17	3.83	2.39	0.94	0.94	0.94	0.00	0.00	0.00	0.00	0.00
Vancouver	Churchill	23.39	13.13	9.94	8.11	5.67	4.07	1.10	0.00	0.00	0.00	0.00
Vancouver	Fergeson	2.03	1.03	0.57	0.57	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Vancouver	Spruce	3.58	0.41	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Vancouver	Yukon	4.58	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Vancouver	CW	25.87	22.00	19.92	17.20	15.97	15.97	14.01	14.01	14.01	14.01	14.01
Vancouver	MK	14.33	10.02	7.87	7.02	6.35	6.35	5.35	3.03	3.03	0.00	0.00
Vancouver	FC	0.34	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Vancouver	QE	3.38	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Vancouver	SH	26.91	21.77	17.59	14.94	9.99	8.40	5.52	3.19	1.80	1.80	1.80
Vancouver	WE	7.62	4.34	3.32	2.41	1.71	0.93	0.00	0.00	0.00	0.00	0.00
Vancouver	DT	1.23	1.12	0.70	0.70	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Percent tree canopy cover for different suburban sites at a spatial extent of 1.5 km^2 (Nominal scale = 1:2400). 1 pixel = 36.0 m^2.

City	Sites	CANOPY PATCH SIZE CATEGORIES										
		A	B	C	D	E	F	G	H	I	J	K
Chicago	Skokie	14.04	6.04	6.04	3.93	2.75	2.31	1.77	1.12	0.99	0.99	0.84
Chicago	S. Evanston	14.19	10.25	6.63	5.14	4.13	3.39	3.03	2.16	2.03	1.88	1.88
Chicago	Wilmette	38.47	36.87	32.93	30.16	28.19	26.77	25.04	24.07	23.45	22.46	21.99
Chicago	N.C. Chicago	4.17	1.78	0.24	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chicago	Lake Forest	53.25	52.43	50.11	48.43	47.39	46.57	45.94	45.70	44.59	44.44	43.58
Chicago	Addison	4.03	1.84	1.02	0.36	0.29	0.15	0.15	0.15	0.15	0.15	0.00
Seattle	Ballard	7.98	2.44	1.27	0.92	0.54	0.43	0.43	0.43	0.43	0.43	0.23
Seattle	Central	32.04	28.26	25.62	24.08	22.43	21.67	21.37	20.86	20.23	19.54	19.54
Seattle	Madronna	17.91	14.69	12.22	10.53	9.12	8.38	7.76	7.44	6.83	6.57	6.41
Seattle	Ravenna	15.14	10.56	8.38	7.51	6.57	6.37	6.14	6.14	6.14	6.14	6.14
Seattle	North End	24.04	19.62	16.56	15.13	14.23	13.51	12.83	12.30	11.98	11.28	10.88
Seattle	Q. Anne	11.15	6.62	4.88	3.76	3.09	2.80	2.56	2.56	2.26	2.26	1.86
Vancouver	Churchill	12.83	6.03	2.79	2.04	1.32	1.21	0.93	0.46	0.46	0.24	0.00
Vancouver	Fergeson	1.29	0.88	0.74	0.63	0.48	0.38	0.14	0.00	0.00	0.00	0.00
Vancouver	Spruce	4.91	1.72	1.15	0.97	0.87	0.65	0.65	0.17	0.00	0.00	0.00
Vancouver	Yukon	3.87	0.29	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Vancouver	CW	19.42	14.75	11.97	10.30	8.83	8.08	7.49	7.14	7.14	6.46	6.46
Vancouver	MK	19.42	14.75	11.97	10.30	8.83	8.08	7.49	7.14	7.14	6.46	6.46
Vancouver	FC	3.01	1.15	0.51	0.28	0.28	0.28	0.15	0.00	0.00	0.00	0.00
Vancouver	CE	8.10	3.99	2.96	2.80	2.65	2.34	1.97	1.67	1.50	1.12	1.12
Vancouver	SH	22.10	17.17	12.51	10.37	8.43	7.78	5.64	5.15	4.59	3.76	3.30
Vancouver	WE	5.21	1.56	0.67	0.34	0.25	0.00	0.00	0.00	0.00	0.00	0.00
Vancouver	DT	0.58	0.23	0.10	0.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Percent tree canopy cover for dsifferent suburban sites at a spatial extent of 25.0 km^2 (Nominal scale = 1:24,000). 1 pixel = 119.0 m^2.

City	Sites	CANOPY PATCH SIZE CATEGORIES										
		A	B	C	D	E	F	G	H	I	J	K
Chicago	Skokie	0.67	0.11	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chicago	S. Evanston	0.57	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chicago	Wilmette	2.03	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chicago	N.C. Chicago	0.19	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chicago	Lake Forest	22.36	14.90	11.76	9.33	8.64	8.17	7.11	7.11	7.11	6.33	6.33
Chicago	Addison	1.27	0.26	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Seattle	Ballard	12.28	11.44	10.64	9.76	9.76	9.76	9.76	9.76	9.76	9.76	9.76
Seattle	Central	8.45	5.83	5.16	3.68	3.25	2.26	2.26	1.51	1.51	1.51	1.51
Seattle	Madronna	6.66	5.29	4.27	4.04	2.56	2.05	1.47	0.78	0.00	0.00	0.00
Seattle	Ravenna	4.94	2.85	2.00	1.32	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Seattle	North End	19.36	13.01	10.64	9.76	9.76	9.76	9.76	9.76	9.76	9.76	9.76
Seattle	Q. Anne	4.00	3.11	2.52	1.97	1.97	1.46	1.46	0.78	0.00	0.00	0.00
Vancouver	Churchill	1.74	0.45	0.30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Vancouver	Fergeson	2.27	1.01	0.47	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Vancouver	Spruce	1.08	0.14	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Vancouver	Yukon	1.08	0.14	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Vancouver	CW	22.39	20.66	20.23	20.23	20.23	20.23	20.23	19.54	19.54	19.54	18.49
Vancouver	MK	22.39	20.66	20.23	20.23	20.23	20.23	20.23	19.54	19.54	19.54	18.49
Vancouver	FC	1.20	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Vancouver	QE	1.20	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Vancouver	SH	1.68	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Vancouver	WE	22.01	20.18	19.38	18.38	17.96	17.96	16.54	16.54	16.54	16.54	16.54
Vancouver	DT	22.01	20.18	19.38	18.38	17.96	17.96	16.54	16.54	16.54	16.54	16.54

Percent tree canopy cover for dsifferent suburban sites at a spatial extent of 85.0 km^2 (Nominal scale = 1:40,000). 1 pixel = 330.6 m^2.

City	Sites	CANOPY PATCH SIZE CATEGORIES										
		A	B	C	D	E	F	G	H	I	J	K
Chicago	Skokie	1.93	0.95	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chicago	S. Evanston	1.93	0.95	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chicago	Wilmette	7.29	2.97	1.53	0.96	0.96	0.00	0.00	0.00	0.00	0.00	0.00
Chicago	N.C. Chicago	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chicago	Lake Forest	26.38	17.35	14.72	10.22	10.22	9.22	6.62	6.62	6.62	4.58	4.58
Chicago	Addison	4.38	1.52	0.49	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Seattle	Ballard	13.17	8.83	6.56	6.25	5.74	5.07	5.07	5.07	5.07	5.07	5.07
Seattle	Central	6.12	2.15	0.86	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Seattle	Madronna	6.12	2.15	0.86	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Seattle	Ravenna	13.17	8.83	6.56	6.25	5.74	5.07	5.07	5.07	5.07	5.07	5.07
Seattle	North End	13.17	8.83	6.56	6.25	5.74	5.07	5.07	5.07	5.07	5.07	5.07
Seattle	Q. Anne	6.12	2.15	0.86	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Vancouver	Churchill	0.39	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Vancouver	Fergeson	8.49	7.47	6.25	6.25	6.25	5.13	5.13	5.13	5.13	5.13	5.13
Vancouver	Spruce	0.39	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Vancouver	Yukon	0.39	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Vancouver	CW	8.43	7.59	7.31	6.26	6.26	5.41	4.26	4.26	4.26	4.26	4.26
Vancouver	MK	8.43	7.59	7.31	6.26	6.26	5.41	4.26	4.26	4.26	4.26	4.26
Vancouver	FC	1.59	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Vancouver	QE	1.59	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Vancouver	SH	1.59	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Vancouver	WE	14.65	9.56	8.65	7.18	5.41	5.41	5.41	5.41	5.41	5.41	5.41
Vancouver	DT	14.65	9.56	8.65	7.18	5.41	5.41	5.41	5.41	5.41	5.41	5.41

APPENDIX H
PERCENT TREE CANOPY COVER FOR SUMMER SURVEY SITES

Percent tree canopy cover for different suburban sites at a spatial extent of 0.2 km^2 (Nominal scale = 1:2400). 1 pixel = 36.0 m^2.

CITIES	SITES	CANOPY PATCH SIZE CATEGORIES										
		A	B	C	D	E	F	G	H	I	J	K
Amherst	MT	48.99	45.02	41.05	39.25	36.25	35.04	34.22	31.48	27.18	27.18	27.18
Amberst	OP	65.47	65.24	64.69	63.76	63.24	63.24	61.78	61.78	60.76	60.76	60.76
Amherst	YT	7.77	7.37	5.87	5.87	5.87	5.29	5.29	5.29	5.29	5.29	5.29
Austin	FP	36.08	30.16	26.50	25.56	25.56	24.69	22.81	21.59	19.00	17.53	17.53
Austio	HP	40.15	38.15	34.02	30.60	29.42	28.71	26.90	25.91	25.91	24.65	24.65
Austin	T	45.27	43.96	41.79	39.88	39.38	37.51	37.51	37.51	37.51	37.51	35.18
Springfield	All Sites	12.19	3.29	0.59	0.59	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Blacksburg	Higbland	35.41	31.85	30.07	28.80	28.80	28.80	28.80	27.63	26.35	26.35	24.63
Blacksburg	Air. Acres	14.98	9.59	5.15	2.92	2.21	1.24	1.24	0.00	0.00	0.00	0.00
Blacksburg	Draper Pres	25.38	17.88	12.68	8.89	7.03	6.21	5.24	5.24	5.24	5.24	3.65
Blacksburg	Terrace V.	2.19	0.63	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Blacksburg	McBryde V.	3.86	1.81	0.41	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Blacksburg	Oak Manor	57.07	56.32	54.56	54.09	53.50	53.50	53.50	52.33	52.33	52.33	52.33
Blacksburg	Blacksburg	49.84	46.82	45.35	44.57	43.42	42.65	42.65	42.65	41.09	41.09	41.09
Chicago	Lake Forest	43.42	42.39	38.02	37.13	33.98	33.98	32.00	29.69	29.69	29.69	29.69
Cbicago	Addison	1.77	0.73	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chicago	N.C. Chicago	3.09	1.08	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chicago	N. Evanston	53.04	51.56	49.42	48.56	47.45	45.87	42.90	40.71	38.07	36.55	36.55
Chicago	S. Evanston	16.43	11.34	5.98	4.23	1.11	1.11	1.11	0.00	0.00	0.00	0.00
Chicago	Skokie	15.85	9.51	5.28	1.24	1.24	1.24	1.24	0.00	0.00	0.00	0.00
Chicago	Wilmette	46.19	44.73	40.87	36.34	32.60	29.56	27.49	26.34	24.94	23.45	23.45
Chicago	Winnetka	40.45	37.71	30.50	27.94	26.10	25.27	24.22	23.00	23.00	20.14	20.14
Vancouver	CW	25.87	22.00	19.92	17.20	15.97	15.97	14.01	14.01	14.01	14.01	14.01
Vancouver	MK	14.33	10.02	7.87	7.02	6.35	6.35	5.35	3.03	3.03	0.00	0.00
Vancouver	DT	1.23	1.12	0.70	0.70	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Vancouver	FC	0.34	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Vancouver	QE	3.38	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Vancouver	SH	26.91	21.77	17.59	14.94	9.99	8.40	5.52	3.19	1.80	1.80	1.80
Vancouver	WE	7.62	4.34	3.32	2.41	1.71	0.93	0.00	0.00	0.00	0.00	0.00
Vancouver	Churcbill	23.39	13.13	9.94	8.11	5.67	4.07	1.10	0.00	0.00	0.00	0.00
Vancouver	Fergeson	2.03	1.03	0.57	0.57	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Vancouver	Spruce	3.58	0.41	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Vancouver	Yukon	4.58	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Percent tree canopy cover for different suburban sites at a spatial extent of 1.5 km^2 (Nominal scale = 1:2400). 1 pixel = 36.0 m^2.

CITIES	SITES	CANOPY PATCH SIZE CATEGORIES										
		A	B	C	D	E	F	G	H	I	J	K
Amherst	MT	32.89	30.03	27.51	25.25	23.20	21.51	20.72	19.61	18.88	18.46	18.01
Amherst	OP	75.91	75.36	74.82	74.49	74.49	74.27	74.01	73.86	73.86	73.86	73.86
Amherst	YT	12.98	12.78	11.06	10.50	10.10	9.67	9.30	8.72	8.19	7.99	7.78
Austin	FP	29.29	23.86	20.58	19.11	17.60	16.40	15.31	14.19	13.25	12.40	12.16
Austin	HP	34.78	32.94	30.52	28.46	27.09	25.79	24.71	23.91	23.55	22.32	21.63
Austin	T	60.69	59.58	58.38	57.03	56.06	54.95	54.14	53.21	52.48	51.88	50.94
Springfield	All Sites	17.76	12.16	10.42	9.99	9.53	9.27	9.17	8.79	8.65	8.65	8.65
Blacksburg	Highland	46.33	44.27	42.65	42.16	41.46	41.19	40.98	40.61	40.48	40.31	40.13
Blacksburg	Air. Acres	5.48	2.97	1.59	0.97	0.80	0.70	0.44	0.28	0.28	0.28	0.28
Blacksburg	Draper Pres	22.22	17.84	14.97	13.35	12.02	11.31	10.42	9.86	9.48	9.18	8.69
Blacksburg	Terrace V.	4.69	2.87	1.85	1.29	1.04	0.88	0.82	0.75	0.75	0.64	0.64
Blacksburg	McBryde V.	4.69	2.87	1.85	1.29	1.04	0.88	0.82	0.75	0.75	0.64	0.64
Blacksburg	Oak Manor	16.17	15.44	14.61	14.41	14.27	14.19	14.19	14.07	14.07	14.07	13.70
Blacksburg	Blacksburg	46.33	44.27	42.65	42.16	41.46	41.19	40.98	40.61	40.48	40.31	40.13
Chicago	Lake Forest	53.25	52.43	50.11	48.43	47.39	46.57	45.94	45.70	44.59	44.44	43.58
Chicago	Addison	4.03	1.84	1.02	0.36	0.29	0.15	0.15	0.15	0.15	0.15	0.00
Chicago	N.C. Chicago	4.17	1.78	0.24	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chicago	N. Evanston	32.07	29.40	26.47	24.21	22.21	20.26	18.91	17.71	16.35	15.22	14.44
Chicago	S. Evanston	14.19	10.25	6.63	5.14	4.13	3.39	3.03	2.16	2.03	1.88	1.88
Chicago	Skokie	14.04	6.04	6.04	3.93	2.75	2.31	1.77	1.12	0.99	0.99	0.84
Chicago	Wilmette	38.47	36.87	32.93	30.16	28.19	26.77	25.04	24.07	23.45	22.46	21.99
Chicago	Winnetka	36.87	34.13	30.05	28.11	27.00	26.17	24.87	22.90	21.26	19.99	19.37
Vancouver	CW	19.42	14.75	11.97	10.30	8.83	8.08	7.49	7.14	7.14	6.46	6.46
Vancouver	MK	19.42	14.75	11.97	10.30	8.83	8.08	7.49	7.14	7.14	6.46	6.46
Vancouver	DT	0.58	0.23	0.10	0.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Vancouver	FC	3.01	1.15	0.51	0.28	0.28	0.28	0.15	0.00	0.00	0.00	0.00
Vancouver	QE	8.10	3.99	2.96	2.80	2.65	2.34	1.97	1.67	1.50	1.12	1.12
Vancouver	SH	22.10	17.17	12.51	10.37	8.43	7.78	5.64	5.15	4.59	3.76	3.30
Vancouver	WE	5.21	1.56	0.67	0.34	0.25	0.00	0.00	0.00	0.00	0.00	0.00
Vancouver	Churchill	12.83	6.03	2.79	2.04	1.32	1.21	0.93	0.46	0.46	0.24	0.00
Vancouver	Fergeson	1.29	0.88	0.74	0.63	0.48	0.38	0.14	0.00	0.00	0.00	0.00
Vancouver	Spruce	4.91	1.72	1.15	0.97	0.87	0.65	0.65	0.17	0.00	0.00	0.00
Vancouver	Yukon	3.87	0.29	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Percent tree canopy cover for different suburban sites at a spatial extent of 25.0 km^2 (Nominal scale = 1:24,000).
1 pixel = 119.0 m^2.

CITIES	SITES	CANOPY PATCH SIZE CATEGORIES										
		A	B	C	D	E	F	G	H	I	J	K
Amherst	MT	47.57	44.08	42.84	42.19	41.45	40.44	39.19	39.19	38.31	38.31	38.31
Amherst	OP	40.31	35.86	34.25	33.67	33.28	31.09	29.28	27.77	27.77	27.77	26.72
Amherst	YT	20.36	18.18	16.61	15.26	14.51	13.49	13.49	12.70	11.81	11.81	10.69
Austin	FP	1.84	0.31	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Austin	HP	2.56	0.76	0.20	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Austin	T	24.89	22.00	20.57	19.77	18.91	17.80	17.34	17.34	17.34	17.34	17.34
Springfield	All Sites	4.20	1.95	0.69	0.69	0.69	0.00	0.00	0.00	0.00	0.00	0.00
Blacksburg	Highland	43.38	39.89	39.16	39.35	37.42	36.52	34.94	34.94	34.94	34.17	34.17
Blacksburg	Air. Acres	43.38	39.89	39.16	39.35	37.42	36.52	34.94	34.94	34.94	34.17	34.17
Blacksburg	Draper Pres	13.06	10.51	8.96	7.75	7.45	5.26	4.70	4.70	4.70	4.70	4.70
Blacksburg	Terrace V.	13.06	10.51	8.96	7.75	7.45	5.26	4.70	4.70	4.70	4.70	4.70
Blacksburg	McBryde V.	13.06	10.51	8.96	7.75	7.45	5.26	4.70	4.70	4.70	4.70	4.70
Blacksburg	Oak Manor	18.82	16.61	14.95	13.37	13.00	12.56	11.39	9.46	8.02	8.02	8.02
Blacksburg	Blacksburg	43.38	39.89	39.16	39.35	37.42	36.52	34.94	34.94	34.94	34.17	34.17
Chicago	Lake Forest	22.36	14.90	11.76	9.33	8.64	8.17	7.11	7.11	7.11	6.33	6.33
Chicago	Addison	1.27	0.26	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chicago	N.C. Chicago	0.19	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chicago	N. Evanston	2.03	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chicago	S. Evanston	0.57	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chicago	Skokie	0.67	0.11	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chicago	Wilmette	2.03	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chicago	Winnetka	5.01	1.87	0.67	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Vancouver	CW	22.39	20.66	20.23	20.23	20.23	20.23	20.23	19.54	19.54	19.54	18.49
Vancouver	MK	22.39	20.66	20.23	20.23	20.23	20.23	20.23	19.54	19.54	19.54	18.49
Vancouver	DT	22.01	20.18	19.38	18.38	17.96	17.96	16.54	16.54	16.54	16.54	16.54
Vancouver	FC	1.20	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Vancouver	QE	1.20	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Vancouver	SH	1.68	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Vancouver	WE	22.01	20.18	19.38	18.38	17.96	17.96	16.54	16.54	16.54	16.54	16.54
Vancouver	Churchill	1.74	0.45	0.30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Vancouver	Fergeson	2.27	1.01	0.47	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Vancouver	Spruce	1.08	0.14	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Vancouver	Yukon	1.08	0.14	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Percent tree canopy cover for different suburban sites at a spatial extent of 85.0 km^2 (Nominal scale = 1:40,000). 1 pixel = 330.6 m^2.

CITIES	SITES	CANOPY PATCH SIZE CATEGORIES										
		A	B	C	D	E	F	G	H	I	J	K
Amherst	MT	36.53	29.47	27.42	25.74	25.01	23.85	22.51	19.47	19.47	17.48	13.19
Amherst	OP	58.44	55.19	53.51	51.27	51.27	51.27	50.07	50.07	46.46	46.46	46.46
Amherst	YT	56.13	52.75	51.11	49.54	49.54	48.50	47.14	44.11	44.11	44.11	44.11
Austin	FP	25.71	20.59	17.51	16.19	15.33	12.86	11.45	11.45	11.45	9.26	9.26
Austin	HP	25.71	20.59	17.51	16.19	15.33	12.86	11.45	11.45	11.45	9.26	9.26
Austin	T	25.71	20.59	17.51	16.19	15.33	12.86	11.45	11.45	11.45	9.26	9.26
Springfield	All Sites	16.46	7.63	5.30	2.30	2.30	2.30	2.30	2.30	2.30	2.30	2.30
Blacksburg	Highland	36.36	32.67	31.38	30.79	29.93	28.93	28.93	28.93	25.49	25.49	25.49
Blacksburg	Air. Acres	36.36	32.67	31.38	30.79	29.93	28.93	28.93	28.93	25.49	25.49	25.49
Blacksburg	Draper Pres	36.36	32.67	31.38	30.79	29.93	28.93	28.93	28.93	25.49	25.49	25.49
Blacksburg	Terrace V.	36.36	32.67	31.38	30.79	29.93	28.93	28.93	28.93	25.49	25.49	25.49
Blacksburg	McBryde V.	36.36	32.67	31.38	30.79	29.93	28.93	28.93	28.93	25.49	25.49	25.49
Blacksburg	Oak Manor	38.76	34.75	33.24	33.24	32.47	32.47	31.26	0.00	0.00	0.00	0.00
Blacksburg	Blacksburg	36.36	32.67	31.38	30.79	29.93	28.93	28.93	28.93	25.49	25.49	25.49
Chicago	Lake Forest	26.38	17.35	14.72	10.22	10.22	9.22	6.62	6.62	6.62	4.58	4.58
Chicago	Addison	4.38	1.52	0.49	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chicago	N.C. Chicago	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chicago	N. Evanston	7.29	2.97	1.53	0.96	0.96	0.00	0.00	0.00	0.00	0.00	0.00
Chicago	S. Evanston	1.93	0.95	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chicago	Skokie	1.93	0.95	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chicago	Wilmette	7.29	2.97	1.53	0.96	0.96	0.00	0.00	0.00	0.00	0.00	0.00
Chicago	Winnetka	7.29	2.97	1.53	0.96	0.96	0.00	0.00	0.00	0.00	0.00	0.00
Vancouver	CW	8.43	7.59	7.31	6.26	6.26	5.41	4.26	4.26	4.26	4.26	4.26
Vancouver	MK	8.43	7.59	7.31	6.26	6.26	5.41	4.26	4.26	4.26	4.26	4.26
Vancouver	DT	14.65	9.56	8.65	7.18	5.41	5.41	5.41	5.41	5.41	5.41	5.41
Vancouver	FC	1.59	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Vancouver	QE	1.59	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Vancouver	SH	1.59	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Vancouver	WE	14.65	9.56	8.65	7.18	5.41	5.41	5.41	5.41	5.41	5.41	5.41
Vancouver	Churchill	0.39	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Vancouver	Fergeson	8.49	7.47	6.25	6.25	6.25	5.13	5.13	5.13	5.13	5.13	5.13
Vancouver	Spruce	0.39	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Vancouver	Yukon	0.39	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

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BIOGRAPHICAL SKETCH

Born in Enugu, Nigeria (Africa), and raised most of my life in Columbus, Indiana (a small, illustrious town situated smack-dab in the cornbelt), I have always been fascinated with animals . . . . Especially animals that live in suburban environments. From cockroaches to pigeons, humans have modified the landscape to the benefit of a few species, but many species cannot live in human-modified environments. Why are some species capable of surviving in these environments and how can we design landscapes to attract more species? These questions led me to study biology at Purdue University where I met Dr. Kerry Rabenold who sparked a desire in me to conduct scientific research on animals.

After receiving my B. S. from Purdue in 1987, I joined the Peace Corps and went to work as a forestry extension agent in Senegal, West Africa. I lived in a Wolof village on the edge of the Sahel desert; it was an experience that changed my life. Learning a unique language and culture and seeing first-hand the social, political, cultural, and ecological difficulties of halting desertification has broadened and matured my perspective on how to resolve ecological problems. The most important lesson that I learned is that any conservation strategy will fail if the local people do not understand and see the importance of a given strategy.

I arrived in Gainesville, Florida, in 1990 and started my graduate career in the Department of Zoology. Still interested in studying animals that live in human-modified environments, I conducted my masters thesis on cockroaches. What fascinating insects that strike such fear and revulsion in the hearts of homeowners! Working with Drs. Carmine Lanciani and Richard Brenner, this research really grounded me in experimental biology and introduce me to the world of science. Then, in 1992, I was introduced to C. S. "Buzz" Holling (my advisor), an extraordinary ecologist who asked questions at large scales outside the realm of traditional, experimental biology. At that time, I was interested in studying how suburban landscapes affect the abundance and diversity of birds; Buzz's way of addressing large-scale questions was appropriate for where I wanted to take my work. The transformation from an experimental biologist to a landscape ecologist was truly "gut-wrenching." I had a difficult time of freeing my mind from the intricacies of small-scale research to the exploratory nature of large-scale research. I will forever remember Buzz's advice, "Mark . . . one must embrace uncertainty."

Along the way of obtaining my Ph.D., I began to recognize the ecological, scientific, and environmental importance of suburban landscapes. Suburban landscapes provide many unique opportunities to study ecological principles, but alas, very few ecologists conduct research in these environments. Further, because of the ever increasing rate of urban sprawl, suburban environments are becoming (if not already) an important factor in the survival of many animal species. A "sea of development" separates many of our protected natural areas and this will affect the future survival of both plants and animals. One goal of mine as a scientist and an educator is to teach people about the importance of designing landscapes "naturally" (e.g., minimize the amount of mowed lawn and the amount of exotic vegetation). In Gainesville, I went and talked to both city and county commissioners in meetings concerning development issues. I also headed-up a team of graduate students, developers, and local citizens to study the effects of a controversial apartment complex on the abundance and diversity of local plants and animals. These experiences opened my eyes to the "gulf" that exists between developers and environmentalists. We truly do not understand "them" and they do not understand "us". We need to build more bridges between these two camps in order promote ecologically and economically sound development.

Stemming from experience in Senegal, I realized that the only way to get homeowners, city planners, and developers to change the way they design suburban areas was for them to truly understand the importance of doing so. For example, how can I suggest to homeowners to not mow their lawns in order to increase the diversity of insects in their backyards when most homeowners think most insects are "icky"? Many people think that insects are not important to humans anyway. My first attempt to reach the general public resulted in a humorous and relevant book titled, "That Gunk on Your Car: A Unique Guide to Insects of the United States." I was amazed at the response this book has received, and I believe that it will expose a broad spectrum of people to the wonderful world of insects. In the future, I plan to continue writing general interest books, teaching, and conducting ecological research in suburban environments. I hope someday to set up a camp that will provide people with the tools and the knowledge to conduct research right in their backyard.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

C S Holling

C. S. Holling, Chair
Eminent Scholar of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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